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THE GENERA OF SUBORDER APOCYNINEAE (APOCYNACEAE AND ASCLEPIADACEAE) IN THE SOUTHEASTERN UNITED STATES²⁰

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ASCLEPIADACEAE R. Brown, Mem. Wernerian Soc. 1: 19. 1811,²¹
"Asclepiadeae," nom. cons.

(MILKWEED FAMILY)

Terrestrial (sometimes in xeric habitats) to aquatic (sometimes in or near fresh, brackish, or salt water), erect to prostrate or scandent and/or twining, perennial or rarely annual herbs (often becoming woody toward base) or sometimes suberect or prostrate subshrubs [or infrequently erect shrubs, trees, or succulents] with usually white latex; axes and leaves glabrous or with various degrees of nonglandular and sometimes glandular pubescence. Leaves simple, opposite or sometimes whorled, subwhorled, subopposite, or alternate, sometimes caducous [and/or, on succulents, often reduced]; blades broad to filiform, apices acute, acuminate, subcuspidate, or mucronate, sometimes obtuse, rarely emarginate, margins often revolute [rarely toothed or lobed], bases attenuate, truncate, hastate, cordate, obtusely sagittate, or auriculate (and clasping stem); petioles distinct, sometimes very short and/or indistinct (especially when leaves linear or filiform), without or very rarely with lateral appendages, bases and/or adjacent areas of stems without or sometimes with usually a few small colleters. Inflorescences terminal but usually appearing lateral and often interpetiolar by sympodial growth, pedunculate to sessile, many- [to rarely 1-]flow-

²⁰Continued from page 401.

²¹According to the title page, this paper was read to the Society on 4 November 1809; according to Stafleu and Cowan (Taxonomic Lit. 1: 366. 1976), preprints were available in 1810. The entry for the Asclepiadaceae in "Nomina Familiarum Bryophytorum et Spermatophytorum Conservanda" (ICBN, 1988) cites pp. 12 and 17, but the family is actually proposed by name on p. 13 (the formal, Latin description begins on p. 19).

ered, cymose but usually appearing umbellate or sometimes racemose, corymbose, or paniculate, bracteate; pedicels longer or rarely shorter than calyces, ebracteolate. Flowers perfect [or rarely carpellate or staminate functionally], sometimes conspicuous, actinomorphic; sepals, petals, and stamens 5, carpels 2. Calyx synsepalous but usually divided nearly to the receptacle, persistent in fruit; lobes usually with squamellae (small, usually scalelike, glandular or non-glandular projections in axils and/or between bases), commonly imbricate to various degrees basally or sometimes valvate, usually acute. Corolla sympetalous, divided nearly to receptacle to sometimes as much as basal $\frac{2}{3}$ united, rotate to sometimes variously campanulate, salverform, urceolate [or funnel-form]; tube [or throat] sometimes with corona (see filaments); lobes alternating with those of calyx, sometimes all overlapping either to right or left in aestivation, but valvate or sometimes imbricate (then all usually not overlapping in a single direction) at anthesis, erect, ascending, spreading, or reflexed. Stamens alternating with the corolla lobes. Filaments connate, forming a column (i.e., tube) surrounding but free from ovaries and styles [or, in the Periplocoideae, distinct from one another but sometimes basally united by an annular or discoid corona], basally adnate to corolla tube [and sometimes throat], short to long, more or less straight, coronas (i.e., abaxial appendages) 1, 2 [or rarely, as in *Eustegia*, 3], often elaborate [or sometimes absent]. Outer (i.e., lower) corona, when present, exceeded by anthers, discoid, entire to variously 5-lobed, basally adnate to but often distinguishable from corolla and apically free, forming a spreading, ascending, or erect annulus at summit of corolla tube. Inner (i.e., upper) corona, when present, exceeding to exceeded by the anthers; segments 5, distinct or less often connate (e.g., in *Matelea*, *Cynanchum scoparium*), each laminate (e.g., in *Cynanchum*, *Matelea*), conduplicate (i.e., hood- or tube-like, as in *Asclepias*), vesicular (e.g., in *Sarcostemma*), or rarely digitate (e.g., in *Cynanchum Northropiae*), sometimes with an adnate appendage adaxially (e.g., horns in *Asclepias*, ligules in *Matelea*) and/or lateral lobes apically (e.g., auricles in *Asclepias*, lateral projections in *Matelea*), stipitate to sessile (i.e., column between corolla and bases of segments visible to not visible, respectively), free from corolla but rarely (e.g., in *Cynanchum clausum*) partially adnate to outer corona. [Coronas in extraregional members as above, or otherwise complex and variable; e.g., in the Periplocoideae, often discoid, adnate to corolla, and bearing anther stalks (i.e., the corona itself is an elaboration of the filament) and/or long, narrow, simple or apically once- or twice-bifurcate and/or coiled lobes]. Anthers each with an apical (and more or less adaxial), hyaline flap inflexed over style-stigma head, unappendaged or (as in *Gonolobus*) appendaged abaxially; united into anther head (i.e., more or less a cylinder or inverted cone) around, adnate to (except along vertical furrows, see below), and mostly concealing lateral surfaces of style-stigma head, immediately subtended by inner corona, or outer corona, or corolla, or (in *Asclepias pedicellata* and *Morrenia odorata*) held well above and separated from inner corona; anther wings from each adjacent pair meeting to form an outwardly projecting slot at plane of contact, enclosing (except for slot) a stigmatic chamber (i.e., enclosed part of vertical furrow including stigmatic and other secretory surfaces); dithecal

and bisporangiate [tetrasporangiate in the Secamonoideae], the contents of each sporangium comprising a single pollinium (i.e., linear pollen tetrads tightly coherent and completely encased by tapetal secretions), 2 of which (1 from each of 2 adjacent anthers) comprising (with translator arms and corpusculum; i.e., hardened secretions of the style-stigma head) 1 pollinarium [or, in the Secamonoideae, 4 of which (2 from each of 2 adjacent anthers) comprising (with relatively undifferentiated secretions of the style-stigma head) 1 pollinarium]. [Anthers in the Periplocoideae mostly without adaxial flaps, unappendaged abaxially; not united into anther head (but sometimes adherent to one another as well as appressed against, often forming a cone above, and concealing style-stigma head), immediately subtended by or held somewhat above corona or corolla; mostly without anther wings; dithecal and tetrasporangiate, the contents of each sporangium (tetrahedral, isobilateral, or sometimes linear pollen tetrads) released at dehiscence into and onto hardened secretions of the style-stigma head (see structures involved in pollen transfer, under style-stigma head of the Periplocoideae, below).] Nectaries near ovaries lacking (but see style-stigma head, below). Carpels completely free in ovule-bearing and stylar regions, united apically into style-stigma head. Ovaries 2, superior to subinferior, simple, distinct, unilocular, each with a marginal placenta; styles short, mostly terete; style-stigma head cylindrical or short-obconic, with convex (and sometimes conical and/or bilobed), flat, or concave (i.e., depressed) apex. Lateral surface of style-stigma head with 5 vertical furrows alternating with the anthers, each with secretions forming: 1 central corpusculum (not concealed by but exceeding to exceeded by the anthers) with 2 attached, pendulous, horizontal [or sometimes erect] translator arms (mostly concealed by anthers), these unbranched and each attached after anther dehiscence to 1 pendulous, horizontal [or erect] pollinium [or, in the Secamonoideae, each apically bifurcate and attached after anther dehiscence to 2 erect pollinia] from each of 2 adjacent anthers to form 1 pollinarium with 2 [or, in the Secamonoideae, 4] pollinia; stigmatic surface within stigmatic chamber (enclosed by anther wings); and nectar. [Style-stigma head in the Periplocoideae short-cylindroid to discoid, with convex (and sometimes conical) or flat apex; lateral surface with 5 approximately vertical areas alternating with the anthers, each with secretions forming structure involved in pollen transfer (adhesive disc attached to base of internally adhesive, inverted, usually elongate cone or partial cone into which individual pollen tetrads fall and are held after anther dehiscence).] Ovules 1 to usually many per locule, often pendulous, anatropous, pseudocrassinucellar, and with a single, massive integument; megagametophyte of the Polygonum type. Fruits follicular, 1 or rarely both carpels developing (the pair, when present, from single flower divergent about 90° or less [or sometimes ca. 160–200°]), lance-ovoid, narrowly fusiform to fusiform-ovoid, acute to attenuate apically, dehiscent along adaxial suture, erect on erect pedicels to pendulous on pendulous ones, sometimes (usually in *Asclepias*) erect on deflexed pedicels; surface tuberculate, winged longitudinally, or smooth, sometimes with short nonglandular and rarely glandular pubescence. Seeds usually many per developed carpel, ovate-lenticular, each usually with a tuft of trichomes at apex;

seed-coat surface papillate or smooth, lateral wings crenate-undulate, variously serrate, or entire; endosperm nuclear, oily and commonly starchy; embryo usually straight, its development of the Solanad type (but see discussion of suborder).²² (Including Periplocaceae Schlechter, 1905.) TYPE GENUS: *Asclepias* L.

Recognized here as distinct from the Apocynaceae (see the discussion of the suborder), the family Asclepiadaceae includes 250 or more genera by most accounts, but with as few as perhaps 50 if the taxonomic concepts developed by Woodson (1941; see below) are applied throughout. Estimates of the number of species have ranged from about 2000 (most authors) to as high as 3000 (Huber). The plants are widespread in tropical and subtropical regions throughout the world but seem to be especially abundant in southern Africa (Huber) and South America (Lawrence). They are both less numerous and less diverse, but still well represented, in the Temperate Zones; nearly 100 genera in the New World north of South America were reduced by Woodson (1941) to nine, five of which are represented in the native flora of the southeastern United States.

Many and perhaps most Asclepiadaceae occur in environments that are from one cause or another water stressful. Several genera in the Old World, most notably *Stapelia* L. (see White & Sloane) and *Sarcostemma* R. Br. (treated here), include succulent-stemmed species with caducous and/or reduced leaves. Most of the species in the Southeast occur in relatively dry, terrestrial habitats; some are found in or near salt or brackish water. A few of our species are adapted to more mesic conditions, and others grow near or in fresh water.

Plants of the Asclepiadaceae are nearly always perennial. They are most commonly herbaceous or variously woody vines, sometimes erect to prostrate herbs, and rarely erect shrubs or small trees. Native representatives in the

²²An excessive and inconsistently applied terminology, especially regarding the flowers, has accumulated over many years. Bookman attempted to standardize the terms used for floral structures in *Asclepias*, and her proposals are generally adopted here. However, because her efforts were based on a single species, her choices are sometimes unacceptable for a genus and/or the family as a whole. For example, she stated that the "culculus" is composed of the "hood" and the "horn," when in fact horns are absent in many species of *Asclepias* and other genera; she also used "bifid fleshy pad" instead of the "alternating lobule" of Woodson (1954), even though in some species of *Asclepias* the structure is not bifid.

In contrast to most others who have studied the Asclepiadaceae, I have chosen not to use "gynostegium" for these plants. I have found the term to be both unnecessary and unclear. For example, Bookman (p. 675) defined the gynostegium as "the union of the stamens with the fleshy stigma head at the flower's center," more or less in accord with Woodson (1941) and others. However, since the various coronas present in the family are considered to be abaxial appendages of the filaments, they would by this definition also have to be considered part of the gynostegium. Bramwell (p. 226) wrote that the "anthers are usually fused to the gynoecium to form a gynostegium," implying that the ovaries are included, while according to Stevens (p. 37) "the gynostegium can be loosely referred to as the androecium plus the style apex but the corolla, below the insertion of the stamens, forms at least the base of the structure."

Other structures for which the terminology has been confused include those here called "style-stigma heads" (see footnote 4) and "colleters" (see footnote 6). The various kinds of coronas present among the Asclepiadaceae in the Southeast are defined in the discussion of *Matelea*.

Southeast include about 17 species in *Cynanchum* L., *Gonolobus* Michx., *Matelea* Aublet, and *Sarcostemma*, all but perhaps three of which (the usually prostrate *M. cynanchoides* (Engelm.) Woodson and *M. pubiflora* (Dcne.) Woodson; the sometimes prostrate *S. cynanchoides* Dcne.) are scandent and/or twining herbs or subshrubs, and perhaps 30 or more species of *Asclepias*, all of which are erect herbs.

The family is also represented in the Southeast by three introduced species of more or less woody vines. *Morrenia odorata* (Hooker & Arnott) Lindley, a native of South America, has become naturalized in Florida, mostly in citrus groves, whereas *Cryptostegia grandiflora* R. Br. and *Periploca graeca* L., natives of Africa and Europe, respectively, seem rarely to have escaped from and/or to have persisted beyond cultivation in Florida but have not become truly naturalized.²³ *Araujia sericofera* Brot., another vine, is grown as an ornamental in both Florida and California but has escaped from cultivation and become naturalized only in California (Spellman & Gunn).

The putatively more primitive Apocynaceae are the closest living relatives of the Asclepiadaceae. In fact, an increasing number of botanists favor uniting the families because there is no sharp distinction between them (see discussion of the suborder). Nevertheless, as represented by plants native to or naturalized in the Southeast, the families are easily distinguished by the presence in the Asclepiadaceae of a number of floral modifications related to pollination. These include, among others, the coronas, anther wings, and pollinia of the androecium, and the hardened secretions of the style-stigma head (i.e., the corpusculum and translator arms) that function in the transport of pollinia. Outside of an indirect connection through the Apocynaceae, the Asclepiadaceae appear to be unlinked to other flowering plants.

Genera of the Asclepiadaceae have been classified on a worldwide basis in a number of systems differing to various degrees in character emphasis, group sequence, and hierarchical arrangement. At the time he initially separated it from the Apocynaceae, Brown subdivided the Asclepiadaceae into three groups. Within each flower the so-called "Asclepiadeae verae" were described as having ten pollen masses, in pairs (the members of each pair from two adjacent anthers), attached to a two-parted, longitudinally furrowed corpusculum on the stigma, as well as connate, abaxially appendaged filaments. The second group, including only *Secamone* R. Br., was unnamed and was said to have 20 pollen

²³*Calotropis procera* (Aiton) Aiton f., a species of erect herbs or subshrubs native to Asia, has been naturalized in the West Indies, as well as along the east coast of South America, for some time (Spellman, 1975b). According to Spellman & Gunn, plants have escaped from cultivation but are evidently not naturalized in the Miami area, although they did not cite, and I have been unable to locate, specimens that would confirm the former.

The flowers of *Calotropis procera* have a corona structure that is unique yet comparable to that of *Asclepias*, particularly members of subg. ASCLEPIODORA (Gray) Woodson (see discussion of *Asclepias*). In *C. procera* each hood appears to be joined to the column for most of its length and is free only at its very short, coiled apex, which is adjacent to the base of the column and much exceeded by the anther head. In *Asclepias* subg. ASCLEPIODORA, on the other hand, each hood appears to be joined to the column for much less than half its length and is otherwise spreading or ascending, with an apex that is uncoiled and only slightly exceeded by the anther head.

masses, in fours (from two adjacent anthers), attached to an unfurrowed corpusculum on the stigma, as well as connate, abaxially appendaged filaments. The third group, the "Periploceae," was described as having five to 20 granular pollen masses (the units or tetrads of each comprising four spheres), with one to four affixed to a single, apically widened corpusculum on the stigma. It is notable that even without completely understanding the structures involved, Brown proposed a classification more in line with current thinking than the majority of those that were subsequently formulated.

Bartling essentially ignored the importance Brown had placed on pollinium number in isolating *Secamone* and thus recognized only two groups in the Asclepiadaceae, the "Asclepiadea genuina," including *Secamone*, with pollinia, and the "Periplocea," without. Lindley, who was probably the first to use the family name in its present form, explicitly adopted Bartling's classification; in fact, most botanists have favored division of the family into two main groups along these lines, although evidence now suggests that the recognition of three may be more appropriate.

Endlicher proposed a system that now appears to reflect suprageneric relationships within the Asclepiadaceae more accurately than does any other. He recognized the three groups proposed by Brown, each as a "subordo," but improved on the latter's scheme by placing the "Periploceae" first, the "Secamoneae" second, and the "Asclepiadeae verae" third.²⁴ The last was divided into three tribes differing in orientation of the pollinia, the "Cynancheae" (pendulous), the "Gonolobeae" (horizontal), and the "Pergularieae" (erect). The "Pergularieae" were separated into two subtribes, the "Hoyeae" and the "Stapelieae," with and without terminal, membranaceous anther appendages, respectively. Divided into groups of unspecified rank and differing in characters of the corolla and corona now thought not to be of value above the generic level were the "Cynancheae" (six groups) and the two subtribes of the "Pergularieae" (two groups each).

Classifications subsequent to Endlicher's included one or more features that now appear to have been regressive, although some included improvements and/or clarifications of the characters used. Decaisne recognized as tribes the three groups proposed by Brown and agreed with Endlicher in placing the "Periploceae" first, the "Secamoneae" second, and the "Asclepiadeae verae" third. However, Decaisne segregated from and placed after the last tribe two additional ones (in order, the "Gonolobae" and the "Stapelieae"), essentially because of differences in the orientation of pollinia, thus obscuring the hierarchy of relationships established by Endlicher. Other characters now thought to be of questionable importance were used to separate the tribes and to divide both the "Asclepiadeae verae" and the "Stapelieae" into a number of named "divisios."

Bentham (in Bentham & Hooker) resurrected Bartling's division of the family

²⁴Article 18.2 (ICBN, 1988) states that names intended for families but published with rank designations such as "ordo" are to be treated as having been published as names of families. This implies that these names of Endlicher should be treated as names of subfamilies.

into two main groups, each a "subordo." The "Periploceae" were followed by the "Euasclepiadeae," which were divided into six tribes. Although differences were indicated between the "Secamoneae," which were placed immediately after the "Periploceae," and the others (e.g., four vs. two pollinia per anther, respectively), they were not reflected in the taxonomy. Some of the remaining tribes differed from one another in orientation of the pollinia: the "Cynancheae" (pendant), followed in order by the "Gonolobeae" (horizontal), and the "Marsdenieae," "Ceropegieae," and "Stapelieae" (all erect). The last three were distinguished on the basis of what are now generally thought to be less substantial characters. Perhaps the most significant of these involved terminal, membranaceous anther appendages, said to be inflexed over the stigmatic disc in the "Marsdenieae," but lacking in the other two. From the "Ceropegieae" the "Stapelieae" were distinguished by their succulent, nearly always leafless stems.

Baillon's system was regressive in two important respects but in some ways contributed to an understanding of the family. Not only was the sequence of suprageneric taxa that had been gaining acceptance essentially reversed, but the hierarchy of relationships was again obscured, in this case by recognition within the family of six "séries." Although it was not reflected in the classification, the first five were said to differ from the last, the "Périplocées," in having pollinia instead of unpackaged pollen. Although this character had been used in previous classifications, Baillon seems to have been among the first to recognize the importance of the fact that the pollen of the "Périplocées" was more or less adherent to an appendage of a corpusculum. Baillon indicated but did not emphasize taxonomically that anthers in the first four "séries" each contained two pollinia, whereas those in the "Sécamonées" produced four. In addition, Baillon implied that corpuscula in the first four "séries" were much larger than those in the "Sécamonées," again affixing a level of importance to this character more in line with current thinking. His reference to apically enlarged anthers in the "Gonolobées" indicates an appreciation of the abaxial appendages now used to distinguish genera within the group (see discussions under *Matelea* and *Gonolobus*).

Schumann recognized as subfamilies two groups within the Asclepiadaceae, the "Periplocoideae" and the "Cynanchoideae," emphasizing not only pollinia but associated structures that contribute to more effective transfer of male gametes in the latter group. A seemingly unnatural distinction was drawn between the "Asclepiadeae" and the other three tribes included in the "Cynanchoideae," based primarily on placement of the pollinia in the basal or the apical part of the anthers, respectively. In addition, the "Asclepiadeae" were divided into five subtribes differing mainly in characters of the corona now thought not to be of value above the level of genus. Perhaps one of the most significant features of Schumann's classification was its unification into a single taxon of all plants with essentially erect pollinia (i.e., the inclusion in the "Tylophoreae" of the "Ceropegiinae" and the "Marsdeniinae"), an arrangement proposed much earlier by Endlicher but mostly ignored otherwise (in fact, the "Tylophoreae" of Schumann is superfluous since Endlicher's "Perularieae" is available for use as the group's name).

Wagenitz's recent treatment of the Asclepiadaceae was patterned closely after Schumann's. Improvements included more explicit descriptions of the subfamilies and tribes and rejection of the subtribes Schumann had included in the "Asclepiadeae." Indeed, Schumann had included *Philibertia* HBK. and *Oxystelma* R. Br. in the "Glossonematinae," *Funastrum* Fourn. in the "Asclepiadinae," and *Sarcostemma* R. Br. in the "Cynanchinae," whereas Woodson (1941) had included all four in the same genus (i.e., *Sarcostemma* sensu lato, as recognized here). In contrast, Wagenitz's decision to recognize as tribes (i.e., the "Marsdenieae" and "Ceropegieae") the subtribes that Schumann had included in the "Tylophoreae" seems less tenable.

Woodson's (1941) extensive contributions notwithstanding, it is often difficult to assess the applicability of his ideas above the level of genus because of the extent to which his studies were limited to North American plants. Nevertheless, it is worthwhile to note his reservations concerning the importance of pollinal orientation in the suprageneric classification of the Asclepiadaceae (see FIGURES 6j; 8d, e, g). Although his concern about the distortion of this feature after removal of the pollinia from the anthers seems irrelevant, it is perhaps significant that he (p. 197) was "willing to be convinced that the normal position of the Gonoloboid pollinium may be truly horizontal," even though his "interpretation of the tribe includes forms with pollinia that range in position from pendulous to ascending."

Woodson (1941) considered the structure of the pollinia to be much more important than their orientation, and primarily on this basis he recognized three tribes of "Asclepiadoideae" in North America: the "Asclepiadeae" and the "Tylophoreae," with pollinia entirely fertile and uniformly rounded or flattened adaxially and abaxially (and pendulous or erect, respectively), and the "Gonolobeae," with pollinia sterile near attachment to the translator arms and either rounded or furrowed on one side and flattened or furrowed on the other (and usually more or less horizontal; occasionally ascending or descending). (See also El-Gazzar & Hamza.)

For reasons elaborated below, it is essentially Endlicher's system that is adopted here, except that the sequence of tribes within his "Asclepiadeae verae" has been reversed and the lower suprageneric groups have been ignored. Thus, recognized here are the Periplocoideae R. Br. ex Endl., the Secamonoideae Endl., and the Asclepiadoideae, and within the last the Pergularieae Endl., the Gonolobeae G. Don, and the Asclepiadeae. Recognition of additional suprageneric taxa is less certain. For example, whereas the subtribes of the Asclepiadeae that Schumann based on characters of the corona are now generally considered to be unnatural (see above), recognition of those that Endlicher included in the Pergularieae on the basis of the presence or absence of the terminal, membranaceous, inflexed anther appendages—that is, the "Hoyeae" (in which he included *Tylophora* R. Br., *Hoya* R. Br., *Marsdenia* R. Br., *Pergularia* L., and 12 other genera) and the "Stapelieae" (in which he included *Ceropegia* L., *Stapelia*, and 13 other genera), respectively—might be justified. Segregation within the latter of a succulent group, corresponding, for example, to the "Stapelieae" of Bentham (in Bentham & Hooker) (in which he included

Stapelia and ten other genera, and from which he excluded *Ceropegia* and ten others), is also worthy of consideration.²⁵

Only the Asclepiadoideae are represented by plants native in the Southeast. *Matelea* and *Gonolobus* (recognized separately for reasons outlined in the discussions of each) belong to the Gonolobeae, while *Cynanchum*, *Sarcostemma*, and *Asclepias* are included in the Asclepiadeae. The latter group is also represented by *Morrenia odorata*, naturalized in Florida, and possibly by *Calotropis procera* (see footnote 23). The Periplocoideae are represented by *Cryptostegia grandiflora* and *Periploca graeca*, each sometimes escaped from cultivation in Florida.

Despite its frequent and perhaps usual inclusion in the Asclepiadoideae, *Secamone* is similar in a number of characters to putatively more primitive taxa within the suborder, justifying placement of the genus in its own subfamily (Safwat). Anthers are four-locular in the Apocynaceae, Periplocoideae, and *Secamone*, but two-locular in the remainder of the Asclepiadoideae. However, Safwat showed that the condition in *Secamone* is not due to the formation of a false partition in each of two essentially two-locular anthers, as Demeter had reported for *Thevetia neriifolia* Juss. ex Steudel (= *T. peruviana* (Pers.) K. Schum.) (Apocynaceae; Plumerioideae), but rather that four groups of arche-

²⁵Sundell provided an annotated list of available and rejected names for taxa between the levels of family and genus in the Asclepiadaceae. According to him, the correct names and author citations for Endlicher's subtribes "Hoyeae" and "Stapelieae" would be Hoyinae G. Don and Stapeliinae G. Don, respectively. Although Sundell did not include them, Endlicher's names should evidently be rejected in favor of Don's because of priority. According to Stafleu and Cowan (Taxonomic Literature, ed. 2, 1976), the pages in Endlicher's *Genera Plantarum* on which his subtribal names appeared were published in August 1838, whereas those in the fourth volume of Don's *A General History of the Dichlamydeous Plants* on which his subtribes "Hoyaceae" and "Stapelieae" appear (according to Sundell) were published no later than April 1838, and possibly as early as 1837. It is essentially for this same reason that Don is cited instead of Endlicher as the author of the Gonolobeae. Not surprisingly, there appear to be no available names between the levels of subtribe and genus for the possible nonsucculent and succulent groups within the Stapeliinae.

According to Sundell, the correct author citation for the Asclepiadoideae as a subfamily of the Apocynaceae (i.e., the Asclepiadaceae as here defined) is Meisner, Pl. Vasc. Gen. 1: 257, 266; 2: 174. 1838. However, according to Stafleu and Cowan (Taxonomic Literature, ed. 2, 1976), these pages were all published in April 1840. In any case, the "Asclepiadoideae" would have been established within the Asclepiadaceae as an autonym with the publication in August 1838 of the Periplocoideae R. Br. ex Endl. and the Secamonoideae Endl. (See also footnote 23.)

It should be noted that Swarupanandan presented a very complex case against some of the names Sundell listed as available. According to this argument, all of the names Sundell indicated as being based on *Pergularia* L. were illegitimate because they were actually based on *Pergularia* R. Br., considered a later homonym and itself therefore illegitimate. For example, although Endlicher cited Linnaeus as the author of *Pergularia* and excluded the species listed under the genus by Brown, he referred only to material from India and China that is excluded from the genus by the selection of material from "Arabia" as typical. Thus, whereas Sundell rejected as superfluous Céropégiées Dcne. (1842), Marsdenieae Benth (1868), and Stapelieae Dcne. (1844) in favor of Ceropegieae Benth (1873), Marsdenieae N. E. Br. (1907), and Stapelieae Benth (1868), respectively, because they all included *Pergularia* and therefore competed with the earlier Pergularieae Endl. (1838), Swarupanandan considered them legitimate because the Pergularieae Endl. is not. If Swarupanandan were to be considered correct, the tribe with erect pollinia recognized here (i.e., the Pergularieae Endl.) would be in need of a legitimate name.

sporial cells are evident in the hypodermis during the earliest stages of internal differentiation.

Demeter had also noted that in the Plumerioideae (Apocynaceae) the four locules are essentially equal in pollen production, but that in the Apocynoideae the abaxial two are partially sterile and perhaps otherwise less developed. He therefore proposed that the bilocular condition in the Asclepiadoideae represented the culmination of a trend involving progressive suppression of the abaxial locules; that is, that the two adaxial locules in the Apocynaceae, Periplocoideae, and Secamonoideae are homologous to the two locules in the Asclepiadoideae. Evidence cited by Safwat supports this (however, see Frye, 1901; Richharia). According to Safwat (p. 110), the two adaxial groups of archesporial cells in the four-locular anther appear "in exactly the same position" as the two in the two-locular condition. In addition, he showed that although the staminal vascular bundle is between the adaxial and abaxial locules in the four-locular anther, it is adjacent to the abaxial epidermis in the two-locular condition.

According to Safwat, the two meiotic divisions of pollen mother cells are simultaneous in most Apocynaceae, most Periplocoideae, and *Secamone*, but successive in all cases investigated in the Asclepiadoideae (e.g., *Asclepias*, *Cynanchum*, *Gonolobus*, *Matelea*, and *Sarcostemma*). The resulting tetrads are usually tetrahedral or isobilateral in the Apocynaceae; generally tetrahedral or isobilateral but sometimes linear (or T-shaped; see Maheswari Devi) in the Periplocoideae; rhomboid and T-shaped in *Secamone* (within pollinia) but perhaps linear as well; and linear (or rarely T-shaped; see Maheswari Devi) in the Asclepiadoideae (within pollinia).

The style-stigma head in *Secamone* also appears to retain certain putatively primitive features according to Safwat, although in my view the supporting generalizations he cited need information from additional taxa. According to Safwat, its entire surface is secretory in the Apocynaceae, although in *Apocynum*, an advanced genus, the secretions in areas alternating with the stamens are loosely organized into five amorphous bodies. At the extreme opposite, in most Apocynaceae—that is, in all Asclepiadoideae investigated but not in *Secamone*—secretions comprising both nectar and complex elements of the pollinaria (i.e., the corpuscula and the translator arms) are limited to well-defined areas within the stigmatic furrows that alternate with the stamens.

The style-stigma heads in the Periplocoideae and in *Secamone* appear to be intermediate between the extremes described above, but in different ways. In the Periplocoideae, as in the Asclepiadoideae, secretions in each of five relatively well-defined areas form structures involved in pollen transfer. In the Periplocoideae these include an adhesive disc that is attached to the base of an internally adhesive, inverted, usually elongate cone or partial cone into which individual pollen tetrads fall and are held after anther dehiscence. On the other hand, in *Secamone*, as in the Apocynaceae, the entire surface of the style-stigma head is secretory, but unlike the condition in *Apocynum*, the secretions in areas alternating with the stamens are tightly organized into structures thought to be homologous with but reduced from those described for the Periplocoideae. Pollen tetrads in *Secamone* are held within pollinia, as in the

Asclepiadoideae, and the inverted or partial cones present in the Periplocoideae do not develop (presumably because they would serve no purpose); instead the hardened secretions in *Secamone* become attached to the pollinia after anther dehiscence in much the same way that the translator arms become attached to the pollinia in the Asclepiadoideae.

Safwat also presented evidence suggesting that the hardened secretions in *Secamone* are homologous only to the corpuscula in the Asclepiadoideae, and that the translator arms of the latter were separately (and perhaps subsequently) evolved. Indeed, I have observed (see illustrations in Schumann) that the structures in *Secamone* are similar in appearance and orientation to corpuscula (i.e., they resemble inverted V's or U's), and that they and the pollinia to which they are attached are very similar to the pollinaria with erect pollinia characterizing the Pergularieae.

In view of the foregoing, I suggest that intercalation of translator arms between the bases of the hardened secretions of the style-stigma head and the bases of the pollinia in *Secamone* (and reduction in the number of pollinia involved from four to two) could have resulted in the condition in the Pergularieae and that within the Asclepiadoideae the erect pollinia of the Pergularieae are most primitive. By similar reasoning, the horizontal pollinia of the Gonolobeae are more primitive than the pendulous ones in the Asclepiadeae. The tribal sequence employed here is intended to reflect these possibilities.

Safwat concluded that his investigations suggested recognition of the Apocynaceae in the broad sense, and within that group the subfamilies Plumerioideae, Apocynoideae, Periplocoideae, Secamonoideae, and Asclepiadoideae. Among recent workers, some (e.g., Stevens) have adopted this arrangement, while others (e.g., Pichon, 1948b) have chosen to recognize an additional subfamily, the Cerberoideae Pichon, near the Plumerioideae and the Apocynoideae (see discussion of the Apocynaceae). However, the case for recognizing the Secamonoideae at the subfamilial level seems more compelling than that for the Cerberoideae. Therefore, while only the Plumerioideae and Apocynoideae are recognized in my treatment of the Apocynaceae, the Periplocoideae, Secamonoideae, and Asclepiadoideae are all accepted here in the Asclepiadaceae, although only the first and third are represented by plants that in the southeastern United States are native, naturalized, or escaped from or persistent beyond cultivation.

As indicated above, the Periplocoideae are generally considered to be more primitive than the Asclepiadoideae, especially with regard to the structures involved in the transfer of male gametes from one flower to another. As mentioned above, secretions from each of five areas on the style-stigma head in the Periplocoideae solidify to form an adhesive disc connected to the base of an internally adhesive, inverted cone or partial cone, into which individual pollen tetrads fall from adjacent anthers and are held after anther dehiscence; this entire unit often becomes attached by the adhesive disc to an insect visitor. In the Asclepiadoideae, secretions from each of five areas on the style-stigma head harden to form a corpusculum and, in addition, two connected translator arms that each become attached after anther dehiscence to one pollinium (the tetrads of one anther locule encased in tapetal secretions) from each of two

adjacent anthers; this entire structure (i.e., pollinarium) frequently becomes attached by the corpusculum to an insect visitor. (See description of pollination in discussion of *Asclepias*.)

The mechanism of pollen transfer in the Periplocoideae is less effective than that in the Asclepiadoideae, due in part to the greater effectiveness in the latter of the corpusculum. Whereas insect parts become attached to the disc just by adhesion, they become wedged—often irreversibly—in an abaxial groove in the corpusculum. In addition, although pollen tetrads are merely adherent to the structures described for the Periplocoideae, in the Asclepiadoideae they are completely enclosed in the pollinia, which are firmly attached to the corpusculum by the translator arms.

The Periplocoideae also differ from the Asclepiadoideae in the extent to which the anthers are associated with one another and with the style-stigma head. Although sometimes adherent to one another, they are not connate into an anther head. In addition, they are appressed against, but not agglutinated to, the style-stigma head. Anthers in the Periplocoideae also lack the wings that characterize the Asclepiadoideae, the adaxial, hyaline flaps present in some Pergularieae and in the Asclepiadeae, and the abaxial appendages of *Gonolobus* (and the extraregional *Fischeria* DC.).

Many aspects of the chemistry, anatomy, embryology, and morphology of the Asclepiadaceae are summarized in the discussion of the suborder. Of taxonomic relevance within the family is Huber's observation that a wide distribution of cardiac glycosides in the Asclepiadeae indicates a "primary position" of the tribe, as well as a close affinity with the Periplocoideae (and the Apocynaceae, especially the Apocynoideae). In other tribes of Asclepiadaceae, these compounds are "gradually" replaced by more specialized types of picric substances. Clearly, a primitive position for the Asclepiadeae within the family is contrary to what has been suggested by morphological evidence (discussed above).

Cytological data regarding the Asclepiadaceae (and Apocynaceae) that had accumulated up to about 1976 were evaluated and summarized to the level of tribe by Stevens. As in the Apocynaceae, the most common and presumably ancestral base chromosome number in the family is $x = 11$; in fact, about 90 percent of the genera and 78 percent of the species for which chromosome counts are available include the sporophytic number $2n = 22$, and only sporophytic numbers based on $x = 11$ have been reported for the Secamonoideae (*Secamone*; $2n = 22$), Pergularieae (20 genera; $2n = 22, 33, 44$, and 66), and Gonolobeae (*Matelea*; $2n = 22$). Other base numbers include $x = 8, 9, 10$, and possibly 12 and 23 , each of which could have been derived from $x = 11$. Although polyploidy in the Periplocoideae, Secamonoideae, and Gonolobeae may be only apparently absent (i.e., due to insufficient sampling), it may be less common throughout the family than in the Apocynaceae (see also Albers).

In general, the Asclepiadaceae are not well known cytologically. For example, of about 300 species thought by Stevens to comprise the Gonolobeae, only a single, extraregional member of *Matelea* is known in this regard (see above). According to data compiled by Bolkhovskikh and colleagues, sporophytic numbers have been reported for, among genera represented in one way or another

in the Southeast, *Asclepias* ($2n = 22$; also 20 and 24), *Calotropis* ($2n = 22, 44$, and 48), *Cryptostegia* ($2n = 24$), *Cynanchum* ($2n = 22$; also 18 and possibly 44), *Periploca* ($2n = 22$ and 24), and *Sarcostemma* ($2n = 22$ and possibly 20).

The Asclepiadaceae are usually considered to be of relatively little economic importance. The seed trichomes are silky but too brittle to be of much use as a textile (Standley & Williams). However, in the southern United States they have been used as a substitute for down, especially in making pillows and cushions (Bramwell). Several uses for these plants have been proposed and to some extent investigated. Particularly during World War II, species of *Asclepias* were evaluated as potential crop plants and sources of alkaloids for oral contraceptives, of latex for the production of rubber, and of stem fibers as substitutes for hemp in rope and paper making (see primarily Whiting; Woodson, 1954). In the year following its construction in 1943, a United States Government "milkweed floss- and seed-extracting plant" in Petoskey, Michigan, using material of (evidently) several species obtained from uncultivated plants in 26 states, provided the military with two million pounds of seed trichomes for use instead of kapok as a stuffing in life-saving equipment (Berkman). Upon restoration of peace, interest in the cultivation of these plants waned, primarily because of their toxicity to livestock (however, see Van Emon & Seiber). Recently there have been evaluations of *Asclepias* for these and related purposes (e.g., Buchanan *et al.*; Campbell; Van Emon & Seiber), as well as a historical account of the many uses of *A. syriaca* (Gaertner).

Many species of Asclepiadaceae, especially those belonging to *Asclepias*, *Cryptostegia*, *Hoya*, and *Stapelia* (among the genera discussed above), are used in horticulture. *Cryptostegia grandiflora* has reportedly been grown as a potential source of natural rubber (Lawrence), although the expenditure of substantial amounts of time and energy on this species during World War II in the Dominican Republic resulted in only one small sheet of rubber (C. E. Wood, Jr., pers. comm.). Many species are toxic to livestock and humans, and the latex of some (especially of *Matelea*, according to Lawrence) is used as arrow poison in Central and South America. Nevertheless, young, tender follicles of several viny species of *Matelea* and other Asclepiadaceae are eaten either fresh or cooked in this same area (Spellman, 1975b; Standley & Williams).

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KEY TO THE GENERA OF ASCLEPIADACEAE IN THE
SOUTHEASTERN UNITED STATES

General characters: *subshrubs, vines, or herbs with latex; leaves simple, opposite, sometimes with colleters; inflorescences terminal but often appearing interpetiolar, cymose but often appearing umbellate; flowers perfect, actinomorphic or nearly so, 5-merous except carpels 2; sepals nearly free, often with squamellae; corollas variously sympetalous, often appendaged adaxially (see filaments), lobes often overlapping; stamens epipetalous, alternating with corolla lobes; filaments connate, forming a column around ovaries and styles, bearing abaxially 1 or 2 coronas; outer corona (when present) usually discoid, basally adnate to corolla, often apically free; inner corona (when present) comprising 5 free or connate, laminate, conduplicate, vesicular, or rarely digitate segments, each sometimes appendaged adaxially; anthers connate into anther head around style-stigma head, subtended by inner corona, outer corona, or corolla; pollen released in pollinia, 2 from adjacent anthers united by 2 translator arms and 1 corpusculum into 1 pollinarium; nectaries within stigmatic chambers, alternating with anthers on style-stigma head; carpels free in ovule-bearing and stylar regions, united apically into style-stigma head; ovaries superior to subinferior, simple, unilocular, with marginal placentae; ovules usually numerous in each carpel; fruits follicles; seeds each with a tuft of trichomes at apex.*

- A. Pollen released as tetrads; corpuscula absent.
 - B. Inflorescences several- to many-flowered; corolla rotate, diameter at apex 2–3 cm; follicles long, narrow, subterete, divergent less than 45° at base, usually erect. [*Periploca graeca*.²⁶]
 - B. Inflorescences few-flowered; corolla funnelform, diameter at apex 5–8 cm; follicles short, stout, angled, divergent ca. 180° at base, usually horizontal. [*Cryptostegia grandiflora*.²⁶]
- A. Pollen released in pollinia; corpuscula present.
 - C. Corpuscula exceeding style-stigma head, translator arms more or less horizontal, pollinia horizontal.
 - D. Anthers lacking abaxial appendages; outer corona absent; inner corona laminate to fleshy, mostly erect, free from corolla, with 15 lobes (usually 5 shallow, obtuse, single, and alternating with 5 longer or sometimes shorter, acute pairs), often with 5 adaxial, adnate, ligulate appendages (opposite each single lobe), exceeding corpuscula (corona in *M. alabamensis* intermediate between inner and outer in position, orientation, fusion to corolla, and morphology). 1. *Matelea*.
 - D. Each anther with an abaxial, fleshy to laminate appendage; outer corona fleshy, mostly spreading, adnate to corolla but free apically (forming a mostly spreading annulus), entire or with 10 lobes (each very shallow and obtuse), unappendaged adaxially, not exceeding corpuscula; inner corona absent. 2. *Gonolobus*.
 - C. Corpuscula not exceeding or (in *Morrenia*) exceeding style-stigma head, translator arms more or less pendulous, pollinia pendulous.
 - E. Inner corona of 5 distinct, vesicular segments; outer corona laminate, spreading, adnate to corolla but free apically (forming an erect or ascending annulus), entire. 5. *Sarcostemma*.
 - E. Inner corona of 5 distinct or basally connate, often conduplicate (and sometimes apically enclosed) but not vesicular segments; outer corona absent.
 - F. Segments of inner corona either digitate and distinct (in *C. Northropiae*) or laminate, flat, and distinct (but basally adnate to corolla in *C. Blodgettii*) or basally connate (in *C. scoparium* and *Morrenia*), without adaxial, adnate appendages; stems twining.
 - G. Segments of inner corona distinct or (in *C. scoparium*) connate to level well beneath that of style-stigma head apex (then corolla lobes less than 2 mm long, leaves linear), glabrous adaxially; anther head immediately subtended by base of inner corona (although segments adnate to corolla in *C. Blodgettii*); bases of leaf blades attenuate, truncate, or cordate. 4. *Cynanchum*.
 - G. Segments of inner corona connate to or above level of style-stigma head apex (and corolla lobes greater than 8 mm long, leaves broad), with nonglandular pubescence adaxially; anther head held well above base of inner corona; bases of leaf blades hastate or less often cordate. 3. *Morrenia*.
 - F. Segments of inner corona fleshy, conduplicate, and distinct, usually with adaxial, adnate appendages (exserted horns) if apically opened; stems prostrate to erect, not twining. 6. *Asclepias*.

²⁶Escaped from or persistent beyond cultivation but clearly not reproducing either sexually or asexually in the southeastern United States. For further discussion, see family discussion.

Subfam. ASCLEPIADOIDEAE [R. Brown ex Endlicher, Gen. Pl. 589. 1838, "Asclepiadeae verae."]

Tribe GONOLOBEAE G. Don, Gen. Hist. Dichlamydeous Pl. 4: 107, 136. [1837?] 1838.

1. **Matelea** Aublet, Hist. Pl. Guiane 1: 277; 3: pl. 109, fig. 1. 1775.

Terrestrial, scandent and/or twining or (in *M. cynanchoides*, *M. pubiflora*) prostrate to suberect, perennial herbs (usually woody toward base) or subshrubs with white latex; axes and leaves with often dense nonglandular and (usually much shorter) glandular pubescence. Leaves opposite; blades ovate, elliptic, lanceolate, or sometimes orbiculate, especially near base of stem, apices acute, acuminate, or sometimes obtuse, rarely emarginate, margins sometimes revolute, bases cordate or obtusely sagittate; petioles distinct, without lateral appendages, bases and/or adjacent areas of stems usually without colleters. Inflorescences pedunculate or (in *M. cynanchoides* and *M. pubiflora*) sessile, 2- (often in *M. cynanchoides* and *M. pubiflora*) to several-flowered, cymose but appearing umbellate, racemose, corymbose, or paniculate, sometimes with both flowers and pedicel scars present simultaneously, bracteate; pedicels longer or (often in *M. cynanchoides* and *M. pubiflora*) shorter than calyces, ebracteolate. Calyx about $\frac{2}{3}$ as long as corolla or less, free nearly to base, usually with both nonglandular and glandular pubescence abaxially, glabrous adaxially; lobes acute, bases imbricate or sometimes valvate, usually with minute squamellae (usually 1 near each sinus). Corolla much shorter than leaves, free nearly to base to united throughout the basal $\frac{2}{3}$, rotate to campanulate, often glabrous or (in *M. pubiflora*) with nonglandular pubescence adaxially, with nonglandular and sometimes glandular pubescence or sometimes nearly glabrous abaxially; lobes valvate or sometimes imbricate, erect, ascending, spreading, or reflexed. Outer corona absent [or, reportedly, sometimes present]. Inner corona exceeding or (in *M. alabamensis*) exceeded by anther head, sessile, cyathiform (segments connate about to level of style-stigma head) and more or less erect (mostly concealing anther head and style-stigma head) and free from corolla or (in *M. alabamensis*) discoid and spreading, free from but in contact with corolla [and/or outer corona]; lobes 5, laminate, each with (or, in *M. cynanchoides*, often without) 2 lateral, shorter to longer projections, and with or without a single, adaxial, adnate, shorter or sometimes equally long appendage (especially the latter giving the appearance of a lobe apex tangentially split into adaxial and abaxial flaps or tongues). Anther head short-obconic, immediately subtended by base of inner corona; anther wing slots directed outward but mostly downward. Anthers each with an apical, adaxial, hyaline flap inflexed over style-stigma head, unappendaged abaxially. Style-stigma head short-obconic, with flat or depressed, distinctly 5-sided apex. Corpuscula clearly exerted from anther head; translator arms mostly horizontal; pollinia horizontal, each with sterile, hyaline tissue adjacent to attached end. Fruits follicular [unknown for many species], 1 (or, reportedly, rarely 2) from each flower, lance-ovoid, narrowly fusiform to fusiform-ovoid, acute to attenuate apically, dehiscent along

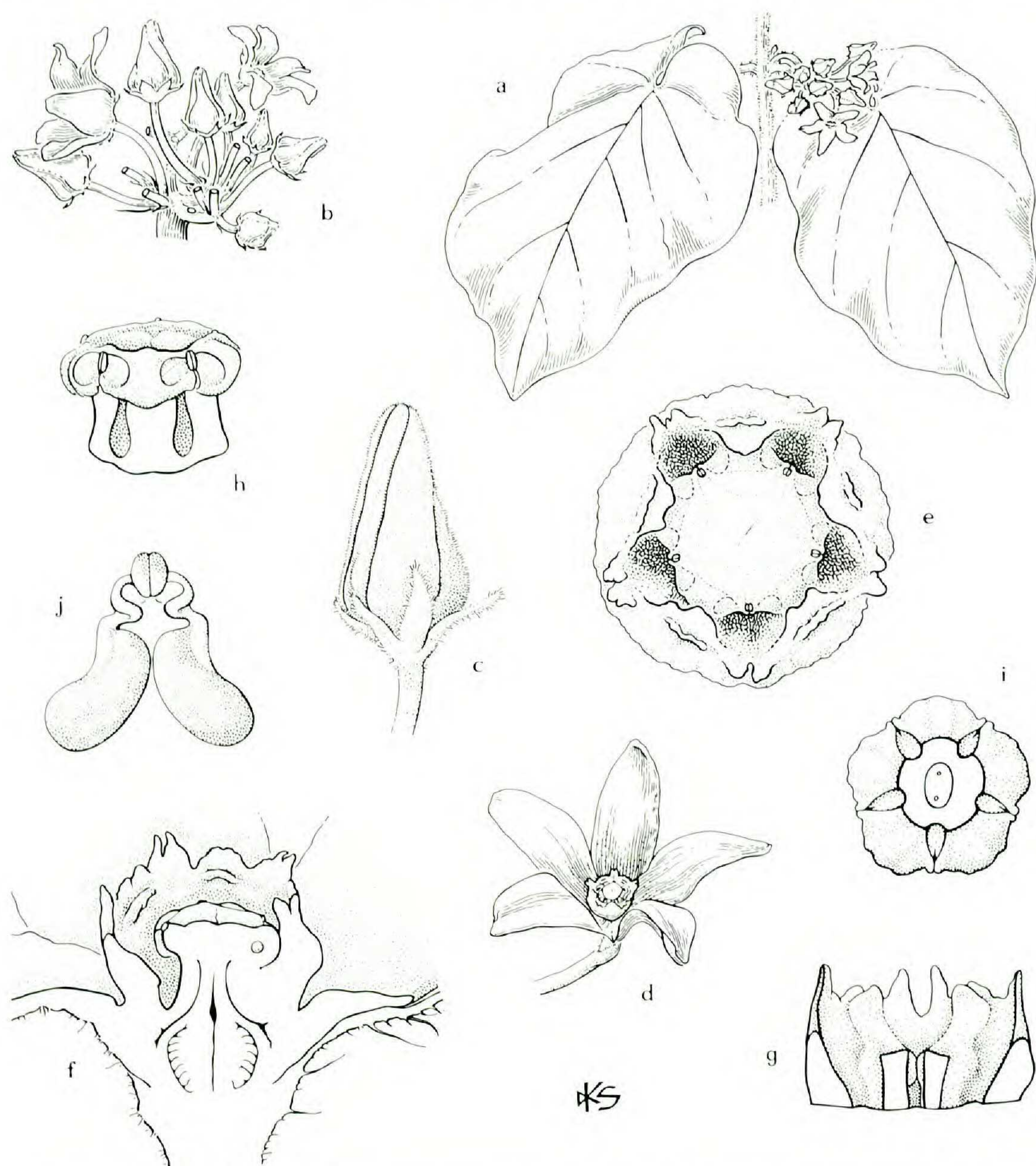


FIGURE 6. **Matelea.** a-j, *M. carolinensis*: a, node, with leaves and terminal inflorescence appearing interpetiolar by sympodial growth, $\times \frac{1}{2}$; b, inflorescence, with pedicel scars and corolla lobes all overlapping to left (clearly seen in only 2 buds, uppermost and rightmost), $\times 1$; c, flower bud, with corolla lobes all overlapping to right, $\times 3$; d, flower at anthesis, with corolla lobes all overlapping to right, $\times 2$; e, flower, from above, without calyx and corolla (5 principal lobes of corona [erect, i.e., perpendicular to page] opposite 5 adaxial ligules [arching over style-stigma head; solid outline, 2 clearly 2-lobed] and 5 apical, adaxial, hyaline anther flaps [inflexed over style-stigma head; dotted outline], alternating with 5 pairs of lateral projections [more or less erect] and 5 corpuscula [between bases of hyaline anther flaps]), $\times 12$; f, flower, cut longitudinally through calyx (1 lobe, of 5, in section, at right), corolla (2 lobes, of 5, in section), androecium (including corona: 2 principal lobes, of 5, and 2 adaxial ligules, of 5, entire, 1 of each in section, at right, immediately subtending anther head; 2 pairs of lateral projections, of 5, entire, each exceeding principal lobes), and gynoecium (both carpels free in ovule-bearing and all but most apical part of styler regions, united apically into style-stigma head), $\times 10$; g, 2 segments, of 5, of corona, removed from flower (2 adaxial ligules in foreground, about equaling 2 principal lobes in background; 1 pair [at center] and 2 single [at left and right] lateral projections exceeding principal lobes), areas of fusion between segments (i.e., between paired lateral projections; leftmost and rightmost) and between segments

adaxial suture, erect on erect pedicels to pendulous on pendulous ones, sometimes erect on deflexed pedicels(?); surface with many or, rarely, a few tubercles [or shallowly winged longitudinally], usually with short nonglandular and glandular pubescence. Seeds many, ovate-lenticular, each with a tuft of trichomes at apex; seed-coat surface papillate or smooth, lateral wings crenate-undulate or entire. (Including *Cyclodon* Small, 1933; *Edisonia* Small, 1933; and *Odonostephana* E. J. Alex. in Small, 1933. Excluding, among others, *Gonolobus* Michx., 1803.) TYPE SPECIES: *M. palustris* Aublet; although Aublet originally included more than one species in *Matelea*, pl. 109, fig. 1, an illustration of *M. palustris*, was cited after the name of the genus. (Name of unknown etymology.)—CLIMBING MILKWEED, SPINY-POD.

Recognized here as distinct from *Gonolobus* Michx. (for reasons summarized in the discussion of that genus, and below), *Matelea* includes a total of 180 to 200 species distributed from the central and southern parts of the United States into South America, according to Spellman (1975b), who treated nine species in Panama. *Matelea* had been considered by most botanists (e.g., Schumann) to comprise less than ten species in tropical South America until Woodson expanded it to encompass North and South American plants to which many other generic names had been applied. In his revision of subg. *Dictyanthus* (Dcne.) Woodson, Stevens indicated that even after the recognition of a few genera of *Gonolobeae* in addition to those favored by Woodson, nearly 200 species of *Matelea* would remain.

Standley & Williams adopted Woodson's circumscription of *Matelea*, but not without certain misgivings. They thought that species in Mexico and Central America that had been placed in the genus in fact represent several genera, and that (p. 450) some of them are "less closely related . . . than certain other" species of *Matelea* are to members of *Gonolobus* and *Fischeria*. Woodson recognized both *Matelea* and *Fischeria* but considered them to be closely related. Murphy also maintained them as distinct, stating that *Matelea* is probably paraphyletic and that uniquely derived character states within *Fischeria* suggest it is monophyletic.

Woodson retained formal taxonomic status for some of the genera he placed in *Matelea* merely because the names were familiar. Mostly on the basis of corollas, coronas, and pollinia, he defined a total of 16 subgenera and six sections, at least some of which were "not entirely satisfactory," according to Stevens (p. 71).

and column (i.e., opposite ligules; at left and right near center, partly defining area opposite stigmatic chambers) not stippled, $\times 12$; h, androecium without corona and gynoecium without ovule-bearing region (2 corpuscula, partly exceeding anther head, opposite and at summit of 2 outwardly projecting slots between anthers and 2 stigmatic chambers [column unmarked; openings in column to stigmatic chambers stippled evenly]), $\times 12$; i, structures shown in "h," seen from below (corpuscula not visible; 5 outwardly projecting slots between anthers external to and opposite 5 stigmatic chambers; apical, connate portion of stylar region at center), $\times 12$; j, pollinarium, abaxial side (1 pollinium from each of 2 adjacent anthers [sterile area near attachment of translator arms unmarked], 2 translator arms, and corpusculum with surface grooved for attachment to insects; pollinia and translator arms more or less horizontal before removal from anthers]), $\times 50$.

Despite recognition of a large number of infrageneric taxa, Woodson included all but one of our species, in addition to a number of others, in subg. *CHTHAMALIA* (Dcne.) Woodson, which he did not further divide and which he considered to be characteristic of the genus in the southern United States and northern Mexico; *Matelea alabamensis* (Vail) Woodson was placed in subg. *Eumatelea* (= subg. *MATELEA*), in the "Reticulatae" (name not validly published). These subgenera are distinguished in Woodson's key (pp. 220–222) primarily by characters of the pollinia ("subquadrate- or oblong-reniform, with a narrow hyaline margin" in subg. *CHTHAMALIA*; "subtriangular-pyriform, with a conspicuous hyaline indentation or margin" in subg. *MATELEA* and three others).

In a biosystematic study of *Matelea* in an area comparable to and perhaps equaling ours, Drapalik recognized nine species, one of which, *M. gonocarpa* (Walter) Shinnars, was included by Woodson—and is included here—in *Gonolobus* (as *G. gonocarpus* (Walter) Perry). Drapalik agreed more closely with Small's treatment (1933) of these plants, in the sense that among them he recognized four groups of species instead of the three favored by Woodson, although he did not think, as Small did, that they should be recognized at the generic level. Thus, he considered *M. gonocarpa*, *M. alabamensis* (*Cyclodon alabamense* (Vail) Small), and *M. pubiflora* (Dcne.) Woodson (*Edisonia pubiflora* (Dcne.) Small) to be, at least morphologically, unrelated to one another or to a group of six closely related species Small (1933) had included in *Odontostephana* E. J. Alex. Comprising what Drapalik called the "Odontostephana group" were *M. Baldwyniana* (Sweet) Woodson, *M. carolinensis* (Jacq.) Woodson, *M. decipiens* (E. J. Alex.) Woodson, *M. flavidula* (Chapman) Woodson, *M. floridana* (Vail) Woodson, and *M. obliqua* (Jacq.) Woodson (in which Drapalik included *M. Shortii* (Gray) Woodson). The species concepts of Drapalik appear to be sound and are adopted here.

I recognize *Matelea* as distinct from and less specialized than *Gonolobus* because of the absence in the former and presence in the latter of abaxial anther appendages. Despite this fact and Drapalik's contention that there are four morphologically unrelated groups involved (even though he included them all in the same genus), plants in our area suggest to me a close link between *Matelea* and *Gonolobus*.

There appear to be four principal types of androecial appendages in the Asclepiadaceae, at least as the family is represented in the Southeast: an outer, discoid, spreading corona that is adnate to the corolla and sometimes shallowly lobed (i.e., the "faucal corona" or "faucal annulus" of many authors, characteristic of, for example, *Gonolobus gonocarpus*); an inner, erect or ascending corona with five principal, distinct or, less often, connate segments (e.g., the hoods of *Asclepias*, the vesicular segments of *Sarcostemma*, the five-lobed, cuplike structures characterizing the "Odontostephana group" in *Matelea*); a whorl of five structures adnate to the adaxial surfaces of the inner corona (e.g., the horns of *Asclepias*, the ligules of *Matelea*); and abaxial anther appendages (as seen in *Gonolobus*). There are, in addition, structures in *M. alabamensis* and *M. pubiflora* that do not entirely fit into any of the foregoing categories and are therefore of particular interest.

That the anther appendages characterizing *Gonolobus* represent abaxial ad-

nations to the stamens of structures homologous to the adaxial ligules of *Matelea* (also considered in the discussion of *Gonolobus*) was rejected by Woodson because of the widespread occurrence in *Gonolobus* of both. Nevertheless, in *G. gonocarpus* the anther appendages are accompanied only by an outer corona; there is evidence neither of an inner corona nor of ligules.

With regard to androecial appendages in general, *Matelea alabamensis* appears to be intermediate in three major respects between *Gonolobus gonocarpus* and members of the "Odontostephana group," which have an inner, cuplike corona with ligules but lack an outer corona. *Matelea alabamensis* approaches *G. gonocarpus* in having a corona that is discoid, instead of cuplike; that is, more like an outer and less like an inner corona. Furthermore, to the extent to which it is adnate to the corolla, the corona of *M. alabamensis* is intermediate between that of *G. gonocarpus*, which is adnate above the point of filament insertion and is therefore a true outer corona, and those of species in the "Odontostephana group," which are not adnate above this point and are therefore true inner coronas. Moreover, the corona of *M. alabamensis* bears ligules that are, relative to those of the "Odontostephana group," less extensively adnate to the corona and more closely associated with the androecium, a disposition that has implications regarding the possibly homologous relationship between the ligules of *Matelea* and the anther appendages of *Gonolobus* (but see below).

Other morphological evidence also suggests a relationship between *Matelea alabamensis* and *Gonolobus gonocarpus*. As indicated in photomicrographs provided by Perry (pl. 494) and drawings included by Drapalik (fig. 7), the pollinaria of these two species are similar in size and morphology, yet they are much larger and of considerably different shape than those of *M. Baldwyniana*, *M. carolinensis*, *M. decipiens*, *M. obliqua*, and *M. pubiflora*, which are among themselves also fairly uniform in these features. In addition, the apex of the style-stigma head tends to be larger and more clearly pentagonal in *M. alabamensis* and *G. gonocarpus* than in our other species of *Matelea*.

It is notable that *Matelea alabamensis* is reportedly quite rare and has not been much collected. Outside of his own specimens, only those obtained by Harbison (on which Vail based the protologue) and by Thorne were known to Drapalik, who indicated after intensive searching that the plants are probably restricted to a few populations near the Apalachicola River in Florida, where the species is considered endangered (Drapalik in Ward), and along the same river in southeastern Alabama and southwestern Georgia (in these places called the Chattahoochee).

Matelea pubiflora is another species Drapalik considered to be isolated from the others he treated, primarily because of its prostrate habit, sessile inflorescences, and campanulate corollas; however, it too suggests a link between *Matelea* and *Gonolobus*. The corona in *M. pubiflora* is similar to that of species in the "Odontostephana group" in being more or less erect, connate around the anther head, not subtended by an outer corona, and not adnate to the corolla. However, it differs in having small, inconspicuous lateral projections on each of the five principal lobes instead of very prominent ones, thus approaching the condition of the discoid, essentially entire outer corona of *G.*

gonocarpus (and *M. alabamensis*). The corona of *M. pubiflora* is also similar to that of *G. gonocarpus* (and *M. alabamensis*) in that it is not entirely erect and is in contact with the corolla. However, the contact in *M. pubiflora* is at least as much due to the campanulate shape of the corolla as to the suberect orientation of the corona; the two structures clearly are not adnate.

Other similarities between *Matelea pubiflora* and *Gonolobus gonocarpus* are evident. Whereas ligules are associated with the inner corona in several species of *Matelea* (including *M. alabamensis*), such structures evidently occur neither on the inner corona of *M. pubiflora* nor on the outer one of *G. gonocarpus*. Thus, it is perhaps significant that according to illustrations provided by Drapalik (fig. 6), the lateral seed-coat wings of *M. pubiflora* and *G. gonocarpus* are crenate and undulate, while those of the other two species depicted, *M. alabamensis* and *M. Baldwyniana*, are nearly entire and flat.

According to Drapalik, *Matelea pubiflora* is most closely allied to species comprising prostrate plants that occur farther west than the area covered in his investigations. In fact, one of these, *M. cynanchoides* (Engelm.) Woodson, has been reported since Drapalik's work from the southeastern United States as we define the region, from Miller County in southwestern Arkansas (Smith), and indeed appears to be related to *M. pubiflora*. Both species are characterized by a prostrate habit, sessile inflorescences, and campanulate corollas, in addition to very small or sometimes nonexistent lateral projections on each of the five principal lobes of a suberect inner corona. That the inner corona bears very prominent ligules in *M. cynanchoides* but is without such structures in *M. pubiflora* (see also above) suggests either that the resemblance between these two species is only superficial or that the taxonomic significance of this character lies at or below the level of species and has been overestimated (see also below).

Matelea pubiflora and *M. cynanchoides* also have smaller leaves than our other species, probably reflecting the drier habitats in which they occur. Drapalik noted that the former is found in more xeric conditions than the other species he treated, and *M. cynanchoides* is known from sandy areas mostly in open woodlands (Correll & Johnston). Whereas *M. pubiflora* is rare and endemic to the Coastal Plain in Georgia and Florida (Drapalik; see also Anderson), *M. cynanchoides* is frequent in northern and central Texas (Shinners, 1964) and is also known from Oklahoma (Correll & Johnston) and, as indicated above, southwestern Arkansas.

Our six remaining species of *Matelea*, the "Odontostephana group" of Drapalik, are indeed closely related. This is an assemblage of scandent and twining vines with large, cordate leaves; essentially rotate corollas; no outer coronas; cyathiform, mostly erect inner coronas with five principal lobes, each with lateral projections and sometimes adaxial (or possibly abaxial, see below) ligules as well; relatively small, cylindrical style-stigma heads; and tuberculate follicles.

Efforts to reveal the true nature of the ligule sometimes present on the inner corona of members of the "Odontostephana group" probably would considerably enhance our understanding of the relationships within *Matelea* and perhaps between this genus and *Gonolobus* as well. According to Drapalik (p. 19), in the six species of this group (and in *M. pubiflora*) "the corona lobes may also have additional small adaxial and abaxial lips, protrusions, or in-

dentations." Clearly, if these structures were in some cases truly abaxial, it would be more difficult to argue that they are homologous to the anther appendages in *Gonolobus* than if they were in all cases truly adaxial. In fact, my own observations suggest that the latter interpretation is more tenable.

In most cases in the "Odontostephana group," the ligules clearly arise from the adaxial surfaces of the inner corona and are exceeded by its principal lobes. However, in many instances the principal lobes instead appear to be apically split into equal adaxial and abaxial halves (see FIGURE 6g); in such cases the former could easily be interpreted as an adaxial ligule that equals the principal lobe. In some instances, and especially frequently in *Matelea floridana*, the smaller, shorter structure (i.e., the apparent ligule) is the outermost, suggesting an abaxial adnation on the principal lobe. In fact, in *M. floridana* (and perhaps other species) the outer structure appears to be the appendage (i.e., ligule) when the corona is viewed from the adaxial side but is just as easily seen as the principal lobe when the corona is observed from the abaxial side. In view of the foregoing, it seems most reasonable to interpret this as yet another adaxial ligule, but one longer than the principal lobe.

Even if the ligules were in all cases truly adaxial, their taxonomic importance (and the likelihood that they are homologous to the anther appendages of *Gonolobus*) is greatly diminished by the degree to which their presence, absence, and size relative to the principal lobes are variable both among and within our six species of the "Odontostephana group." For example, each species and in some cases individual flowers have both ligulate and nonligulate principal lobes. In addition, whereas the ligules were shown to exceed the principal lobes in perhaps 13 of 17 illustrations of *Matelea floridana* provided by Drapalik (fig. 2), my own examination of three herbarium specimens evidently belonging to this species (as determined by Drapalik and by me, using his key, but see below) revealed this condition on only one. Although in 12 of 13 drawings of *M. carolinensis* (Drapalik's fig. 2) the ligules were exceeded by the principal lobes, among four herbarium specimens I saw they much exceeded them (i.e., the principal lobes appeared as abaxial ridges) on one and were about equal to them (i.e., as in FIGURE 6g) on two others. It seems likely that with enough observations each of the conditions described above would be represented in each of the six species.

The foregoing examples involving closely related species (i.e., *Matelea cynanchoides* and *M. pubiflora* on one hand, and those in the "Odontostephana group" on the other) suggest that the ligule is of limited or no taxonomic value in *Matelea*. Indeed, although Drapalik documented with illustrations much of the variation he observed, the character was used in neither the key nor the formal descriptions he provided. In contrast, the abaxial anther appendages invariably absent in *Matelea* and present in *Gonolobus* appear to represent a much more stable character, one by which these genera can consistently be distinguished. The differences in stability between the ligules of *Matelea* and the abaxial anther appendages in *Gonolobus* imply genetic differences, which in turn suggest that the structures are not strictly homologous.

The closely related species in the "Odontostephana group" differ mainly in aspects of the corolla and corona that are often difficult to discern on living

plants and are nearly impossible to observe in herbarium material. These include, among others, color of corolla and corona, size and shape of corolla lobes, and shape and size of the lateral projections relative to the principal lobes of the inner corona. As Drapalik documented extensively, the shapes and relative sizes of these structures, particularly the lateral projections, are frequently and irreversibly distorted by drying. He therefore stated that the correct assignment to species of herbarium specimens is frequently impossible and that liquid-preserved flowers should be included by collectors when possible. I have frequently observed in herbarium material both color distortion and the loss of significant portions of the lateral projections, the latter evidently due to shriveling in life and/or upon drying.

Matelea floridana supposedly differs from the other species in the "Odontostephana group" in that the principal lobes of the inner corona usually exceed the lateral projections. According to Drapalik, the species is rare and endemic to the Coastal Plain in northern Florida, although the possibility that it may occur in southeastern Georgia should be investigated because of the presence there of open or dense oak-hickory (*Quercus-Carya*) mixed hardwood forests. Wunderlin and colleagues have recently reported the species from central Florida. Drapalik reported that *M. floridana* occurs in shadier conditions than do other members of this group, and the later flowering observed among plants of this species in nature was maintained in common-garden experiments.

The lateral projections usually equal or exceed the principal lobes in the remaining five species in the "Odontostephana group." Two of these supposedly differ from the rest in having rotate-reflexed or rotate instead of rotate-ascending corollas; *Matelea carolinensis* and *M. flavidula* are very similar but can be distinguished on the basis of corolla-lobe color (usually dark maroon vs. some shade of green or rarely light maroon, respectively) and the relative lengths of the principal corona lobes and the lateral projections (the lateral projections always longer in *M. carolinensis*, see FIGURE 6f, g; the structures usually about equally long in *M. flavidula*). Both species are evidently infrequent and occur in open or second-growth oak-hickory forests, but *M. carolinensis* appears to have a wider geographic range (see, however, Wunderlin *et al.*). Whereas this species occurs in various floristic provinces from Delaware to Texas, *M. flavidula* is restricted to the Coastal Plain in South Carolina, Georgia, Florida, and Alabama.

*Matelea Baldwyniana*²⁷ usually differs from the other two species with rotate-ascending coronas (*M. obliqua* and *M. decipiens*) in its white corollas; flowers with cream-colored corollas also occur in *M. Baldwyniana* and, rarely, *M. obliqua*, but the lateral projections of the corona lobes are usually much longer in *M. Baldwyniana*. The corollas of *M. obliqua* are otherwise normally rose colored, light maroon, or infrequently dark maroon or green, while those of *M. decipiens* are always dark maroon; in addition, the corolla lobes of *M. obliqua* are usually four to six times as long as wide, whereas those of *M. decipiens* are nearly always stouter.

²⁷According to Drapalik, application of this name is based on common, modern usage; type material has not been found, and the species is not now known from the type locality, near Savannah, Georgia.

Matelea Baldwyniana is rather common in northwestern Arkansas and adjacent parts of Missouri, particularly in places close to springs, but it is rare east of the Mississippi River; in addition to Arkansas, the species is known in our area only from Alabama and Florida. *Matelea obliqua* and *M. decipiens* are infrequent over large areas in the eastern United States: *M. obliqua* approximately from Georgia north to Missouri and Pennsylvania; *M. decipiens* from Georgia north to Maryland and west to Texas.

Drapalik reported that for most species of *Matelea* included in his investigation, vegetative growth in nature was greatest in either exposed or partially shaded conditions, but that in garden experiments partial shade was optimal for *M. carolinensis*, *M. decipiens*, and *M. obliqua*. Flowering was not observed among the few individuals (species not indicated, probably indeterminable) found in places with northern exposures. It is thought to occur under dense shade only in *M. alabamensis* and *M. floridana* (as well as *G. gonocarpus*), which flower under very exposed conditions as well.

All species of *Matelea* that Drapalik studied are evidently best adapted to well-drained soils, and none is found in areas subject to inundation. *Matelea pubiflora* and *M. cynanchoides* occur in drier conditions than the other species; according to Drapalik, *M. pubiflora* (he did not study *M. cynanchoides*) has especially large taproots and is restricted to communities dominated by turkey oak (*Quercus laevis* Walter) and long-leaf pine (*Pinus palustris* Miller). With the exception of *M. cynanchoides*, our species of *Matelea* are usually found in or at the edges of forests dominated by oaks, hickories, and other hardwoods.

Drapalik also reported the pH of soil samples obtained within 15 cm of the surface at each of his study sites. All of the samples associated with *Matelea Baldwyniana* and *M. obliqua* and most of those collected with *M. carolinensis* and *M. decipiens* were basic to circumneutral. In contrast, a majority of those obtained for *M. alabamensis*, *M. flavidula*, *M. floridana*, and *M. pubiflora* were acidic, although Drapalik reported growing plants of all four species from seed to flowering in pH-neutral substrates.

Drapalik reported natural pollination involving plants both in and out of cultivation for each of the species included in his study except *Matelea pubiflora*; observation during daylight hours revealed no insect visitors to flowers of this species, although numerous fruits were produced by plants in cultivation. Visitors with attached pollinaria were in all cases small flies belonging to the Anthomyiidae, Chloropidae, Milichiidae, and Phoridae. Indeed, the flowers were said to emit the kinds of odors (i.e., unpleasant, at least to most humans) and in many cases to have the colors (i.e., reds, maroons) to which such insects are attracted. The flies have been observed to effect pollination while feeding on nectar produced by the flowers.

The details of pollination as described by Drapalik are very much like those presented here for *Asclepias*, with a few notable exceptions. Although nectar is produced in the stigmatic chambers in both genera, in *Matelea* it accumulates at the base of the inner corona immediately outside the base of the outwardly projecting slot, instead of in the hoods at either side. In many but not all cases involving species of *Matelea*, pollinator parts appear not to be wedged into the corpusculum, as they evidently always are in *Asclepias*, but instead to adhere

to it even though corpuscular secretions have not been noted. In *Matelea*, in contrast to *Asclepias*, the anther wings are much smaller and more rigid and the pollinia are larger than the slot opening, so that pollinia are not and need not be inserted completely but merely placed against the slot. Nevertheless, as in *Asclepias*, the convex side must be adjacent to the opening for successful pollen-tube growth.

In nature all of our species of *Matelea* appear to be reproductively isolated, with the exception of *M. carolinensis* and *M. decipiens* of the "Odontostephana group." Drapalik reported populations of these two species and various intermediates between them throughout Georgia and the Carolinas. He specifically mentioned genetically unmixed populations of *M. carolinensis* in Tennessee, Maryland, and Virginia, and of *M. decipiens* in Louisiana and Missouri, but did not address the issue for the remaining geographic areas in which these species occur. Drapalik attributed the infrequency of interspecific hybridization to various factors, including temporal, geographic, ecological, and mechanical isolation. Evidence suggested that pollinator specificity was of limited importance in this regard.

Breeding experiments conducted by Drapalik in cultivation using the six species belonging to the "Odontostephana group" indicated that each is self-incompatible (a gametophytic system was assumed) but revealed little about the relationships among them. Artificial cross pollinations involving six of the 15 possible species pairs were successful in the sense that mature fruits and viable seeds were produced. Although fruit set among plants in cultivation was greater than that observed in nature (6.10 vs. 0.22 fruits per plant), the overall percentage of successful interspecific pollinations among them was low (6.84 percent). This observation, together with the fact that successful artificial crosses between *Matelea carolinensis* and *M. decipiens* were no more frequent than those between species not known to hybridize in nature, diminishes the reliability of these results. Nevertheless, it is tempting and perhaps reasonable to suggest that additional attempts might eventually result in successful crosses between all pairs of species in this group. This is especially so because the percentage of successful pollinations between species was equal to that observed between individuals from different populations of the same species, indicating that interfertility between and within species might be approximately equal. A lower rate of success resulted from pollinations within single populations of a given species, presumably due to self-incompatibility and a greater genetic similarity among the individuals. As expected, an even lower success rate was obtained from self-pollinations.

Compared to the parents, the F_1 hybrid plants resulting from artificial pollinations were intermediate in flower color and morphology (Drapalik). In addition, the hybrids were as fertile as the parents, as determined by pollen stainability, the number of seeds per fruit, and seed viability. Drapalik provided helpful illustrations of coronas representing the parents and progeny involved in several of the interspecific crosses. Unfortunately, this documentation does not elucidate the genetic basis of ligule variation.

Matelea carolinensis is cultivated in North America with sufficient frequency

to have been treated by Bailey and colleagues. Drapalik provided instructions for growing all species found in the southeastern United States, both from seed and by transplanting mature plants.

REFERENCES:

Under references for the Apocynineae, see ANDERSON; BAILEY *et al.*; CORRELL & JOHNSTON; SCHUMANN; SMALL (1933); SMITH; and STANDLEY & WILLIAMS.

Under references for the Asclepiadaceae, see DRAPALIK; MURPHY; PERRY; SHINNERS (1964); SPELLMAN (1975b); STEVENS; WARD; and WOODSON.

VAIL, A. M. Studies in the Asclepiadaceae.—VII. A new species of *Vincetoxicum* from Alabama. Bull. Torrey Bot. Club **30**: 178, 179. pls. 9, 10. 1903. [= *M. alabamensis*.]

WUNDERLIN, R. P., B. F. HANSEN, & D. W. HALL. The vascular flora of central Florida: taxonomic and nomenclatural changes, additional taxa, II. Sida **13**: 83–91. 1988. [According to annotations by DRAPALIK, *M. floridana*, but not the previously reported *M. carolinensis*, present.]

2. *Gonolobus* Michaux, Fl. Bor. Am. **1**: 119. 1803.

Terrestrial, scandent and/or twining [or sometimes prostrate], perennial herbs (usually woody toward base) or subshrubs with white latex; axes and leaves nearly glabrous or with usually sparse nonglandular and sometimes (usually much shorter) glandular pubescence. Leaves opposite; blades ovate, elliptic, or sometimes suborbiculate especially near base of stem, apices acute, acuminate, or subcuspidate, sometimes obtuse, rarely emarginate, margins not revolute, bases cordate or obtusely sagittate [sometimes obtuse or cuneate]; petioles distinct, without lateral appendages, bases and/or adjacent areas of stems usually without colleters. Inflorescences pedunculate [or subsessile], few- to several-flowered, cymose but appearing umbellate, racemose, or corymbose, bracteate; pedicels longer than calyces, ebracteolate. Calyx about $\frac{1}{2}$ as long as corolla or less, free nearly to base, sometimes with nonglandular pubescence abaxially, glabrous adaxially; lobes acute, bases valvate, with minute squamellae (usually 1 near each sinus). Corolla much shorter than leaves, free nearly to base to united throughout the basal $\frac{1}{3}$, rotate [to subcampanulate], usually with at least some degree of nonglandular pubescence adaxially, glabrous abaxially; lobes valvate, spreading to reflexed [or sometimes erect to ascending]. Outer corona discoid, fleshy, crenate-undulate, basally adnate to the corolla tube but apically free, forming a mostly spreading [or erect] annulus. Inner corona absent [or reportedly exceeded by anther head, substipitate, essentially discoid and spreading, free from but in contact with outer corona and/or corolla; lobes 5, laminate but sometimes revolute, unappendaged]. Anther head short-obconic, immediately subtended by base of outer [or inner] corona; anther wing slots directed outward but mostly downward. Anthers each with an apical, adaxial, hyaline flap inflexed over style-stigma head, and an apical, abaxial, fleshy, appendage projecting outward. Style-stigma head short-obconic, with flat or depressed, distinctly 5-sided apex. Corpuscula clearly exerted from anther head; translator arms mostly horizontal; pollinia horizontal, each with sterile, hyaline tissue adjacent to attached end. Fruits follicular [unknown for many species], 1 from

each flower, lance-ovoid, narrowly fusiform to fusiform-ovoid, acute to attenuate apically, dehiscent along adaxial suture, erect on erect pedicels to pendulous on pendulous ones, sometimes erect on deflexed pedicels; surface winged longitudinally [or sometimes reportedly with tubercles], usually with sparse, nonglandular pubescence. Seeds many, ovate-lenticular, each with a tuft of trichomes at apex; seed-coat surface papillate or smooth, lateral wings crenate-undulate. (*Vincetoxicum* Walter, 1788, nom. illeg., not Von Wolf, 1776, not Moench, 1794.) LECTOTYPE SPECIES: *G. gonocarpus* (Walter) Perry²⁸ (*Vincetoxicum gonocarpum* Walter); Perry (*Rhodora* 40: 283. 1938) selected *G. macrophyllus* Michx. as the “standard-species,” a name, as she correctly recognized, invalidated by Michaux’s citation in synonymy of the earlier *V. gonocarpum*. (Name from Greek, *gonia*, angle, and *lobos*, pod, evidently in reference to the longitudinally winged (i.e., angled in transverse section) follicles of the first (and the type) but not the other two species originally included by Michaux.)—ANGLE-POD.

Recognized here as distinct from *Matelea* (for reasons put forth in the discussion of that genus, and below), *Gonolobus* includes perhaps 100 species (Spellman, 1975b). Although most of these occur in Mexico and Guatemala, *Gonolobus* is distributed from the southeastern United States and nearby areas, where it is represented by a single species, *G. gonocarpus* (Walter) Perry, to Panama, where fewer than ten species are known.

The correct name and appropriate circumscription of this genus have been unclear as well as controversial. As proposed by Michaux in 1803, *Gonolobus* included three species. *Vincetoxicum gonocarpum* Walter (as *V. gonocarpos* Walter) and *V. acanthocarpum* Walter (as *V. acanthocarpos* Walter), comprising the totality of *Vincetoxicum* Walter (Fl. Caroliniana, 104. 1788) as originally delimited, were listed as synonyms of the first two, *G. macrophyllus* Michx. and *G. hirsutus* Michx., respectively (thus invalidating these two names of Michaux), while the third, *G. laevis* Michx., was newly described.

Although it is generally conceded that the material on which *Gonolobus laevis* was based actually represents more than one species, interpretations regarding it are confusing and/or in some cases contradictory. Gray (p. 75) partially described *G. laevis* with the phrase “folliculis laevibus 5-angulatis,” suggesting that he chose portions agreeing with Michaux’s description of *Gonolobus* (“folliculi plerumque costati seu angulosi”) but contradicting the latter’s concept of *G. laevis*. Although Michaux had explicitly indicated that the fruits of *G. macrophyllus* and *G. hirsutus* are angled and muricate, respectively, he had described (p. 75) those of *G. laevis* merely with the phrase “folliculis laevibus,” implying that they are smooth and not angled. According to Woodson, the material selected by Gray is probably conspecific with *G. gonocarpus*.

Unlike Gray, Vail chose material contradicting Michaux’s generic concept but agreeing with his description of *Gonolobus laevis*. She maintained that such

²⁸Because *Gonolobus* is masculine, the correct epithet is *gonocarpus*, even though *gonocarpos* was used initially in this combination by Perry and has been employed by nearly everyone since. Similarly, *Vincetoxicum* is neuter, so the epithet in this case should be *gonocarpum*, even though *gonocarpos* had been proposed initially by Walter and, again, widely used thereafter.

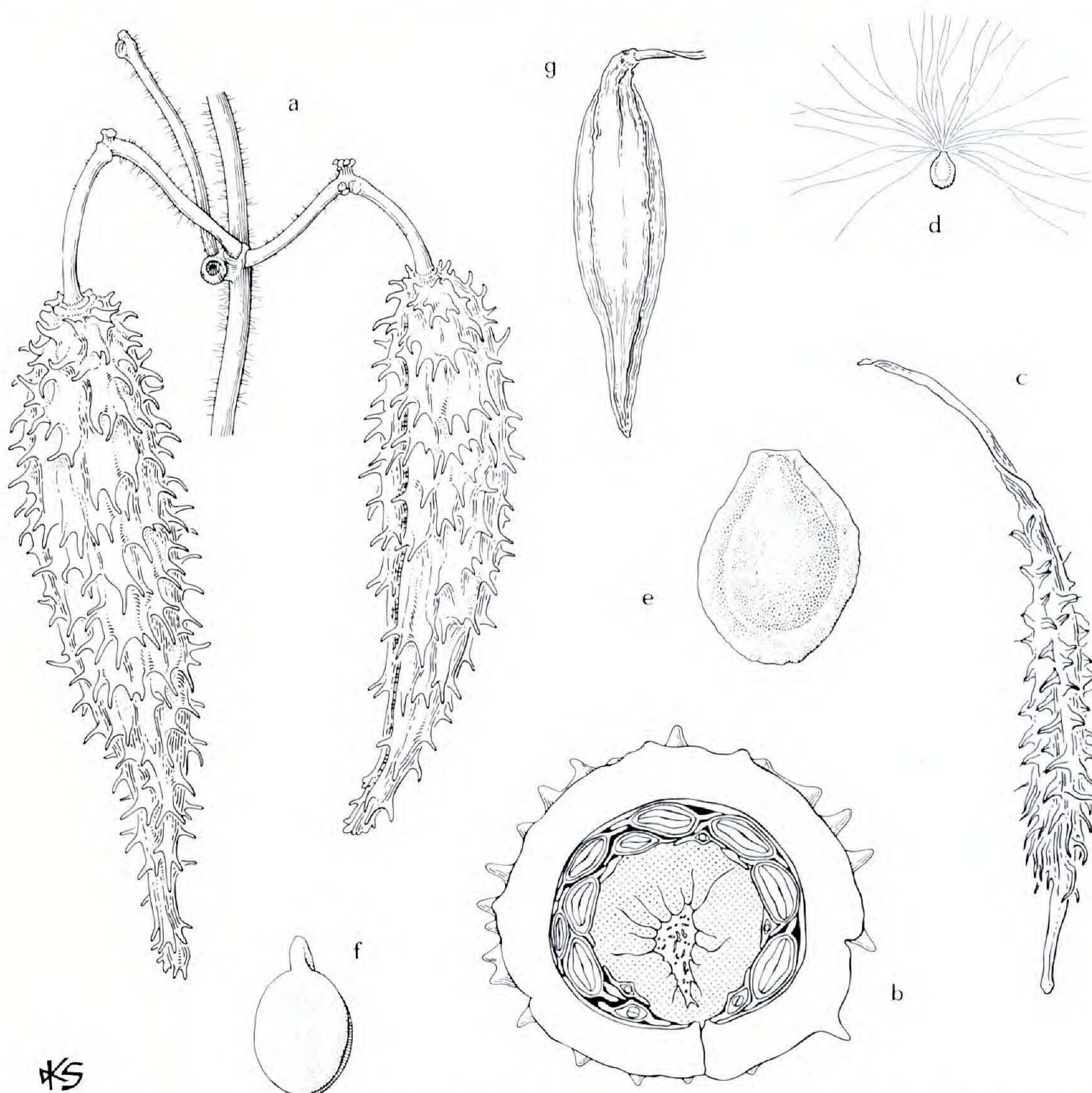


FIGURE 7. **Matelea** and **Gonolobus**. a-f, *M. carolinensis* (from flowering material collected earlier): a, 2 mature follicles, from 2 flowers of 1 inflorescence, surfaces tuberculate, $\times \frac{3}{4}$; b, mature follicle, cut transversely (pericarp and laterally winged seeds unmarked; area of compacted, apical tufts of trichomes stippled evenly; marginal placenta near center), $\times 2$; c, placenta, after release of seeds, $\times 1$; d, seed, with apical tuft of trichomes, $\times \frac{1}{2}$; e, seed, apical tuft of trichomes removed, seed coat winged laterally, $\times 3$; f, embryo, somewhat expanded from soaking in water (oriented as in "e"), $\times 3$. g, *G. gonocarpus*: mature follicle, surface winged longitudinally, $\times 2$.

material was much more abundant than that selected by Gray but nevertheless assignable to *Enslenia albida* Nutt. (= *Cynanchum laeve* (Michx.) Pers.). Her assessment accords better with "The guide for the determination of types" (ICBN, 1983; element T.4.e) and is now generally accepted, although it is difficult to determine "current usage" in this case.

Vail logically returned to *Vincetoxicum* Walter the first two species included in *Gonolobus* by Michaux (see above), leaving in the latter only *G. laevis*. Vail's interpretation of this species was adopted by, for example, Small (1933), but not by Perry, who accepted Gray's interpretation but nevertheless reestablished the original concept of *Gonolobus* by selecting Michaux's first species, *G. mac-*

rophyllus (= *G. gonocarpus*), as the type of the genus. This designation is especially significant because of nomenclatural problems with Walter's *Vincetoxicum*.

Both the name and the description of *Gonolobus* provided by Michaux suggest that he envisioned a group of plants with angled (i.e., longitudinally winged) follicles, so it seems inconsistent for him to have indicated such a condition in only the first of the three species descriptions he included. In doing this he might have been simply following Walter, who had done essentially the same both in naming and in describing the two species comprising his *Vincetoxicum* (viz., *V. gonocarpos* and *V. acanthocarpos*, the epithets meaning angled and thorny fruit, respectively) but did not address the issue in his generic description.

The second species included in *Gonolobus* by Michaux, *G. hirsutus* (*Vincetoxicum acanthocarpos*), was placed by Alexander (in Small, 1933), together with six other species of the southeastern United States in *Odontostephana* E. J. Alex., in synonymy under *O. carolinensis* (Jacq.) E. J. Alex. Although the descriptions (p. 1076) indicated that the follicles in *Vincetoxicum* (here *Gonolobus*, for reasons given below) and *Odontostephana* were "unarmed, wing-ridged toward the apex" and "armed with fleshy spines," respectively, the genera were separated in the key (p. 1065) on the basis of corona structure, primarily "disk-like or saucer-shaped" in the former and "cup-shaped or incurved at the tip" in the latter (Small, 1933). *Odontostephana* was included in an expanded *Matelea* Aublet by Woodson, and Michaux's second species is now generally known as *M. carolinensis* (Jacq.) Woodson (see discussion of *Matelea*).

The correct generic name for the first species listed by Michaux (i.e., the one with longitudinally winged follicles) remained in doubt for several reasons. Although *Vincetoxicum* Walter (1788) preceded *Gonolobus* Michx. (1803), it would have been eliminated as a *nomen rejiciendum* if a proposal to conserve *Vincetoxicum* Moench (1794) had been adopted (see Perry). Although the latter did not occur, *Vincetoxicum* Walter is to be considered a later homonym and therefore illegitimate on the basis of Ross's argument that *Vincetoxicum* Von Wolf (1776) had in fact been validly published, so *Gonolobus* now appears to be correct.

As indicated above, there has been in addition to the nomenclatural confusion a considerable amount of taxonomic disagreement regarding *Matelea* and *Gonolobus*. It is perhaps surprising that the genera usually have been combined by botanists dealing with the relatively few species in North America (e.g., Clewell; Correll & Johnston; Duncan & Kartesz; Jones & Coile; Radford *et al.*; Shinnars, 1950, 1964; Smith; Steyermark) but retained as separate by those treating plants in Central America (e.g., Spellman, 1975b; Standley & Williams), where the two genera are better represented and evidently less distinct.

Woodson chose to maintain both *Gonolobus* and *Matelea* despite drastically reducing (from 97 to nine) the number of asclepiadaceous genera represented in the New World outside of South America. Although he stated that differences between the two in corona structure did not exist, he maintained that the fleshy, abaxial appendages of the anthers universally present in *Gonolobus* do not occur in *Matelea* and thus based his separation primarily on this character. He

considered the possibility that the anther appendages of *Gonolobus* represented adnations to the stamens of structures corresponding to the ligules often adnate to or at least associated with the adaxial side of the corona in *Matelea*, but he rejected the idea because such structures "almost invariably" occur in *Gonolobus* in addition to the anther appendages. It is notable that ligules nevertheless do not occur in *G. gonocarpus* (see also discussion of *Matelea*).

Woodson cited fruit and pubescence characters as further support for his generic separation. For the relatively few species of each genus for which fruits were known, he stated that those of *Gonolobus* are usually winged, while those of *Matelea* are usually muricate (i.e., angled and thorny, respectively, in the sense of Walter). He also pointed out that a mixture of long, nonglandular and short, glandular trichomes is unique to most members of *Matelea* (and possibly the closely related if not congeneric *Fischeria* DC.) and never found in *Gonolobus*.

Shinners (1950), who believed that *Matelea* and *Gonolobus* are not sufficiently distinct for separation at the generic level, provided a rebuttal to Woodson's position. He reported that the follicles of *M. producta* (Torrey) Woodson (western Texas to southern Arizona and northern Mexico) are not at all muricate (they are smooth but evidently not angled or winged, according to Correll & Johnston), and that those of *M. reticulata* (Gray) Woodson (central, southern, and western Texas; northeastern Mexico) are only sparingly so. Indeed, I have seen a specimen of *Matelea* obtained in Florida (Curtiss 5948; GH), probably belonging to *M. flavidula* (Chapman) Woodson (based on the key provided by Drapalik) that bears a single follicle with only a few short projections; although it does not appear to have been angled before pressing, an intermediacy between the genera in fruit is nevertheless suggested.

My observations of both glandular and nonglandular trichomes on specimens of *Gonolobus gonocarpus* are consistent with those reported by Shinners (1950) for this species and for the probably conspecific *G. suberosus* (L.) R. Br. as well (see below), except that it seems to me that pubescence in general is not as substantial in this species as it is in our representatives of *Matelea*. Shinners (1950) also cited other evidence suggesting that *Gonolobus* and *Matelea* are not distinct, at least in Texas.

Shinners (1950) regarded the presence of anther appendages in *Gonolobus* and their absence in *Matelea* to be insufficient grounds for separating the two genera, citing Woodson's (p. 239) observation that the structures in the former were "rather poorly developed as a rule in the temperate representatives." However, although those of *G. gonocarpus* evidently are not as elaborate as those of some more tropical species, they are nevertheless quite apparent and unlike any structures present in *Matelea*.

Drapalik studied nine of these species in the southeastern United States, including *Gonolobus gonocarpus* (as *Matelea gonocarpa* (Walter) Shinners) and eight other species here included in *Matelea*. He believed (p. 80) that all nine should be included in the same genus because of "many similarities" among them, despite the fact that the follicles of *G. gonocarpus* and the others are "quite different." His concession that glandular trichomes are relatively scarce on plants of *G. gonocarpus* is consistent with my observations (as indicated

above), and I agree that trichome density should not be used as a generic distinction. However, I do not agree with his implication (p. 80) that the anther appendage present throughout *Gonolobus* and completely lacking in *Matelea* also fails in this regard merely because it is "simply a sterile enlargement . . . that protrudes outward." Characters of the androecium, primarily a variety of sterile enlargements of the filaments (i.e., coronas), have served as the morphological bases for many and perhaps most genera of Asclepiadaceae, including all those in the Southeast.

Despite the taxonomic decision to recognize a single genus, Drapalik stated that *Gonolobus gonocarpus* was not morphologically related to the eight species of *Matelea*. He also reported several other differences between them, involving aspects of physiology, phenology, and ecology. He found greater susceptibility to infections by fungi and rusts in *G. gonocarpus* than in the six species of the "Odontostephana group" (see discussion of *Matelea*), among cultivated (but not wild) plants, and reported a fragrance (presumably floral) in *G. gonocarpus* unlike any in the other eight.

Drapalik also determined that in garden plots individuals of *Gonolobus gonocarpus* were always the first to resume growth in the spring, yet they flowered later than adjacent plants belonging to the "Odontostephana group" of *Matelea*. Although he reported some overlap in flowering between *G. gonocarpus* and members of the "Odontostephana group," he found that of six possible hybrids (among 99 flowering individuals grown from seeds resulting from natural pollinations of the cultivated plants), none showed evidence of parentage by *G. gonocarpus*. According to Drapalik, when plants of *G. gonocarpus* and species of *Matelea* occur together in nature, those of the former usually are found in the moister conditions and flower a bit later (except that *M. floridana* evidently flowers at about the same time or earlier). At least in the Southeast, plants of *G. gonocarpus* occur in a wider range of substrate moisture and pH than do individual species of *Matelea* and, as in the case of only two of our species of *Matelea* (*M. alabamensis* and *M. floridana*), flower under conditions ranging from densely shaded to sunny. This wider ecological amplitude would account, at least in part, for the fact that *G. gonocarpus* appears to be more abundant in the Southeast than any of the species of *Matelea*.

While Drapalik's position in combining *Matelea* and *Gonocarpus* is certainly not without merit or support from other botanists, it resulted from study of only nine of the perhaps 300 species in question. Despite the existence of southeastern species of *Matelea* (*M. alabamensis* and *M. pubiflora*) that I believe are in several ways intermediate between the genera (see discussion of *Matelea*), my studies support the decisions of those familiar with all of the plants involved (e.g., Spellman, 1975b; Standley & Williams; Stevens, pers. comm.; Woodson) to recognize both *Matelea* and *Gonolobus*.

Gonolobus gonocarpus (as *Vincetoxicum gonocarpos* Walter) and *G. suberosus* (L.) R. Br. (as *V. suberosum* (L.) Britton) were both recognized in the southeastern United States by Small (1933), but according to Drapalik, the Linnaean epithet has been misapplied and the plants are certainly conspecific. The species have been separated on the basis of corolla-lobe size and pubescence, those in *G. gonocarpus* being more than twice as long as the calyx lobes (vs. twice as long or less) and glabrous (vs. pubescent) adaxially. However, on

the basis of these characters, Drapalik found both species and "every conceivable intermediate" in several populations and grew both from seeds of a single fruit obtained from a plant in Tennessee. Drapalik emphasized that any endeavors to interpret the considerable morphological variation in this species taxonomically should be preceded by adequate field (and, presumably, other biosystematic) study.

Woodson recognized three subgenera²⁹ in *Gonolobus*, one of which, the extraregional subg. "Pseudolachnostoma," has erect or ascending (vs. spreading or reflexed) corolla lobes and lacks the outer, discoid, annular corona present in the other two. Anthers in the extraregional subg. "Pterolobus" are supposedly partially exerted from the style-stigma head, while those in subg. "Eugonolobus" are not.

Gonolobus gonocarpus occurs throughout the southeastern United States with the exception of southern Florida, in all states bordering our area, and in Illinois and Indiana. The plants often occur in low, moist, rich but well-drained areas with hardwood trees in swamps and on floodplains.

Gonolobus gonocarpus is of sufficient horticultural interest in North America to have been treated by Bailey and colleagues, and Drapalik provided instructions for growing the plants both from seed and by transplantation. According to Standley & Williams, the tender young fruits of Central American species of *Gonolobus* (and related genera) are commonly eaten as vegetables and are sold for this purpose in markets in Guatemala City.

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Under references for the Apocynineae, see BAILEY *et al.*; CLEWELL; CORRELL & JOHNSTON; DUNCAN & KARTESZ; JONES & COILE; RADFORD *et al.*; SMALL (1933); SMITH; STANDLEY & WILLIAMS; and STEYERMARK.

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Tribe ASCLEPIADEAE [R. Brown ex A. P. de Candolle, Bot. Gallicum **1**: 323. 1828.*]

3. **Morrenia** Lindley, Bot. Regist. **24**(Misc.): 71. 1838.

Terrestrial, scandent and/or twining subshrubs with white latex; axes and leaves with often dense nonglandular pubescence. Leaves opposite; blades ovate, elliptic, or lanceolate, apices acute or acuminate, margins sometimes undulate,

²⁹The names of these subgenera were not validly published by Woodson, since they were accompanied in 1941 neither by a Latin description or diagnosis nor by a reference to a previously and effectively published Latin description or diagnosis (i.e., they were not published in accordance with Art. 36.1 [ICBN, 1988], the effective date of which is 1 January 1935). Therefore, they are enclosed in quotation marks here.

rarely revolute, bases hastate or less often cordate; petioles distinct, without lateral appendages, bases and/or adjacent areas of stems usually with a few colleters. Inflorescences short-pedunculate, few-flowered, cymose but appearing racemose or sometimes subumbellate, bracteate; pedicels longer to shorter than calyces, ebracteolate. Calyx ca. $\frac{1}{2}$ – $\frac{2}{3}$ as long as corolla, free nearly to base, glabrous or with nonglandular pubescence abaxially, glabrous adaxially; lobes acute, bases valvate, usually with 2 or 3 squamellae near each sinus. Corolla much shorter than leaves, free nearly to base, salverform (but with lobes much longer than tube, and therefore appearing nearly rotate), glabrous adaxially and abaxially; lobes valvate, spreading to reflexed, the margins revolute. Outer corona absent. Inner corona exceeding anther head, stipitate, cyathiform (segments connate about to level of or above style-stigma head), erect (concealing anther head and style-stigma head), free from corolla; lobes 5, each with 2 lateral, shorter projections near sinuses between segments, and either emarginate, with (as viewed from the adaxial side) a mucronate convexity at base of emargination, or entire, with acute, marginally incurved apices. Anther head cylindrical, held well above [or sometimes immediately subtended by] base of inner corona; anther wing slots directed outward. Anthers each with an apical, adaxial, hyaline flap inflexed over style-stigma head, unappendaged abaxially. Style-stigma head short-obconic, with conical, bilobed apex. Corpuscula clearly exerted from anther head; translator arms mostly pendulous; pollinia pendulous, each completely fertile. Fruits follicular, 1 from each flower, lance-ovoid to ovoid, obtuse or truncate and often mucronate apically, dehiscent along adaxial suture, mostly pendulous on pendulous pedicels; surface smooth or sometimes shallowly winged longitudinally [or rugose], usually with short nonglandular and glandular pubescence. Seeds many, elliptical-lenticular, each with a tuft of trichomes at apex; seed-coat surface rugose, lateral wings crenate-undulate or entire. TYPE SPECIES: *M. odorata* (Hooker & Arnott) Lindley (*Cynanchum odoratum* Hooker & Arnott), the only species initially included in the genus by Lindley. (Named for Charles Morren, 1833–1886, professor of botany and director of the botanical garden at Liège, Belgium.)—MILKWEED VINE, STRANGLER VINE.

A genus of probably two species. *Morrenia odorata* (Hooker & Arnott) Lindley is native to Paraguay, southern Brazil, and northern and central Argentina but has escaped from cultivation and become naturalized in Florida and perhaps elsewhere (see below), whereas *M. brachystephana* Griseb. is evidently restricted to northern and central Argentina. Compared to the latter, *M. odorata* has larger flowers (e.g., corollas 10–15 vs. 5–6 mm long), stipitate (vs. sessile) anther heads, and smooth (vs. rugose) follicles (see, for example, Fabris; Schumann).

Details are uncertain regarding the introduction to Florida of *Morrenia odorata* (see primarily Tucker *et al.*), a species favored by horticulturists for the vanillalike fragrance of its flowers (Ryan & Knorr). An individual was reportedly cultivated in Pasco County in 1939, and plants were first reported from citrus groves, clearly the preferred habitat in the adventive range of the species,

in Orlando in 1957. The species is now widespread in central peninsular Florida but is most abundant in Lake, Orange, and Seminole counties. In addition to citrus groves, where they are both numerous and problematic, the plants have been infrequently observed in other man-made and/or disturbed habitats. They have been found in natural habitats as well, albeit rarely.

Morrenia odorata is a perennial, vigorously growing vine that in Florida often kills support plants, particularly citrus trees, through both shading and girdling (hence, "strangler vine"); parasitism evidently does not occur (Ryan & Knorr), although individuals compete for water and nutrients (Spellman & Gunn). Infestations by *M. odorata* also reduce the efficiency of irrigation, spraying, and harvesting in citrus groves.

Control of *Morrenia odorata* has been difficult, and further spread of the weed seems likely for several reasons (see primarily Tucker *et al.*). The plants produce an abundance of viable, wind-dispersed seeds (about 1000 per fruit) at a young age (two years or less) and also propagate vegetatively from root fragments resulting from tillage. They have been known to survive freezing temperatures and have demonstrated high degrees of tolerance to the chemical herbicides registered for use in citrus groves.

Biological control of *Morrenia odorata* is complicated by the presence of latex, which renders the plants (and most members of the suborder) toxic or at least unpalatable to most animals. Woodhead and co-workers reported that populations were reduced by more than 90 percent within one or two years after citrus plants were somehow "treated" in 1978, 1979, and 1980 with a fungus, *Phytophthora palmivora* (E. J. Butler) E. J. Butler. Mitchell & Kann-wischer-Mitchell determined that applications under citrus trees of 1.5 chlamydospores per square centimeter of soil resulted in the death of over 95 percent of the plants of *M. odorata*. Nevertheless, the species evidently continues to be a serious problem.

Singh & Achhireddy studied germination and seedling growth to gain a better understanding of the biology and therefore the possibilities for control of *Morrenia odorata*. They found that germination rates were markedly reduced above and below pH 7—to zero percent after seven days at pH 8.0 and pH 5.5; on either side of a 20/25°C (12-hour) thermoperiod, although seedling growth was highest at about 30°C; and at soil depths greater than 2.5 and less than 0.5 cm. Both germination rates and seedling growth decreased with decreasing water potential.

Allelopathic effects on *Morrenia odorata* have been suspected of *Lantana Camara* L. (Verbenaceae), native to tropical America and the Coastal Plain in the Southeast, but also a serious weed in citrus groves in Florida. In fact, Achhireddy & Singh found that incorporation into the soil of dried material of *L. Camara* significantly inhibited vegetative growth in *M. odorata* (e.g., 50 percent seedling mortality within 15 days of germination in soil containing, in terms of dry weight, one percent root material of *L. Camara*), although it had no apparent effect on final germination percentages.

Morrenia odorata is one of several species of Asclepiadaceae reported to be used in South America to stimulate lactation in cattle and humans. The latex

is used in the manufacture of cheese, while people in the Chaco region of Argentina eat the follicles either raw or cooked (see Spellman & Gunn).

REFERENCES:

Under references for the Apocynineae, see SCHUMANN.

Under references for the Asclepiadaceae, see FABRIS; SPELLMAN & GUNN; and SUNDELL.

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WOODHEAD, S. H., W. H. RIDINGS, C. L. SCHOULTIES, R. K. CLARK, & N. E. EL-GHOLL. Field efficacy of *Phytophthora palmivora* for control of milkweed vine. *Phytopathology* **71**: 913. 1981.

4. *Cynanchum* Linnaeus, Sp. Pl. 1: 212. 1753; Gen. Pl. ed. 5. 101. 1754.

Terrestrial to semiaquatic (sometimes at edges of salt marshes), scandent, perennial herbs (usually woody toward base) [or erect to prostrate subshrubs] with white latex; axes and leaves glabrous or with various degrees of nonglandular pubescence. Leaves opposite, sometimes caducous and the plants leafless or nearly so; blades ovate, elliptic, lanceolate, linear, or filiform, apices acute, acuminate, or mucronate, margins often revolute, bases attenuate, truncate, or cordate; petioles distinct, sometimes very short and/or indistinct (especially with linear or filiform leaves), without lateral appendages, bases and/or adjacent areas of stems sometimes with a few small colleters. Inflorescences pedunculate or sessile, few- to many-flowered, cymose but appearing umbellate and/or racemose, bracteate; pedicels longer than calyces, ebracteolate. Calyx about $\frac{1}{2}$ as long as corolla or less, free nearly to base, usually with nonglandular pubescence abaxially, glabrous adaxially; lobes acute or sometimes subotuse, bases variously imbricate, with minute squamellae. Corolla much shorter than leaves, free nearly to base to united throughout the basal $\frac{1}{3}$ (in *C. Blodgettii*, *C. Northropiae*), campanulate (but lobes mostly free), campanulate-salverform (in *C. Northropiae*), or campanulate-urceolate (in *C. Blodgettii*), glabrous or with dense, nonglandular pubescence adaxially (in *C. Blodgettii* and *C. Northropiae*), glabrous abaxially; lobes valvate or variously imbricate, erect proximally but ascending, spreading, or reflexed distally. Outer corona absent. Inner corona exceeding or (in *C. scoparium*) exceeded by anther head, stipitate to substipitate or sessile, comprising distinct or (in *C. scoparium*) basally connate, erect to ascending segments, each basally free from or (in *C. Blodgettii*) adnate to corolla [or rarely absent]; segments 5, laminate or (in *C. Northropiae*) fleshy and subterete (solid, not conduplicate), apically acute, subobtuse, or (sometimes in *C. angustifolium*) emarginate, or (in *C. laeve*) with 2 linear, erect lateral append-

ages. Anther head cylindrical, immediately subtended by or (in *C. Blodgettii*) seemingly (by adnation) separated from base of inner corona; anther wing slots directed outward. Anthers each with an apical, hyaline flap erect to arching over style-stigma head, unappendaged abaxially. Style-stigma head short-cylindric, with flat, conical, or bilobed apex. Corpuscula exceeded by anther head; translator arms subhorizontal; pollinia pendulous, completely fertile. Fruits follicular, 1 or sometimes 2 from each flower (the pair, when present, from single flower usually divergent less than 90°), narrowly fusiform to fusiform-ovoid, acute to attenuate-caudate apically, dehiscent along adaxial suture, erect on erect pedicels or pendulous on pendulous ones; surface smooth (or reportedly sometimes in *C. laeve*) winged longitudinally, with various degrees of non-glandular pubescence. Seeds many, ovate-lenticular, each with a tuft of trichomes at apex; seed-coat surface usually smooth, lateral wings entire or remotely crenate. (Including, among others, *Ampelamus* Raf., 1819; *Amphistelma* Griseb., 1861, at least in part; *Epicion* Small, 1933; *Enslenia* Nutt., 1818, at least in part; *Enslinia* Reichenb., 1828, at least in part; *Gonolobus* Michx., 1803, in part; *Lyonia* Ell. non Nutt., of the Ericaceae, 1821; *Mellichampia* Gray, 1887; *Metalepis* Griseb., 1866; *Metastelma* R. Br., [preprinted 1810] 1811, at least in part; *Roulinia* Dcne., 1844; *Rouliniella* Vail, 1902; and *Tylodontia* Griseb., 1866.) LECTOTYPE SPECIES: *C. acutum* L.; see Meyer, Comment. Pl. Afr. Austral. 216. 1837 [1838]. (Name from Greek, *kynos*, dog, and *ancho*, to strangle or lace up, perhaps in reference to the similarity of the plants in morphology and in use to those of *Apocynum*, and possibly to their usually lianous habits, as well.)—VINE MILKWEED, SAND VINE.

Considered here in the broad sense, *Cynanchum* comprises 200 or more species (Spellman, 1975b) in tropical and to lesser extents temperate regions throughout the world. As with some of our other genera of Asclepiadaceae, *Cynanchum* owes its large size mainly to the taxonomic reorganization of the family by Woodson. Small (1933) had placed our five species, all indigenous in the Southeast, in five separate genera, the names of which comprise only a minority of those now generally considered to be synonymous with *Cynanchum*.

As originally proposed by Linnaeus, *Cynanchum* included five species. Only one or, depending on taxonomic interpretation, two of these were retained in the genus by Brown, who nevertheless included a total of 15 species in six unnamed "sections" that he thought would eventually be accepted as genera. Indeed, genera were subsequently proposed for many of Brown's "sections," as well as for other plants now generally thought to be congeneric. The consolidation of these genera appears to have begun with Schumann, who in reverting to a system more in line with Brown's, included under *Cynanchum* 11 generic synonyms (and over 100 species) that had been in use for plants throughout the world. Woodson listed two of these genera plus 21 other generic synonyms for plants in North and Central America and stated that several more eventually would be added for species in South America.

It is difficult to know how Schumann's concept of *Cynanchum*, which he assigned to subtribe Cynanchinae of tribe Asclepiadeae, compares to the one employed here. Only one of our species, *C. laeve* (Michx.) Pers., was actually

mentioned in his treatment of the family, and it was included (as *Enslenia albida* Nutt.) in a different subtribe of the Asclepiadeae, the Asclepiadinae. (For this reason and others, these subtribes are not recognized here; see family discussion.) Some of our other species were included, for example, by Small (1933), in genera also separated from *Cynanchum* by Schumann: *C. Blodgettii* (Gray) Shinnars was placed in *Metastelma* R. Br., and *C. scoparium* Nutt. was included in *Amphistelma* Griseb.; Schumann included *Amphistelma* in *Metastelma*, which he placed with *Enslenia* in the Asclepiadinae. Small (1933) included *C. angustifolium* Pers. (as *C. palustre* (Pursh) Heller) in *Lyonia* Ell. (non Nutt.), which was ignored by Schumann, and *C. Northropiae* (Schlechter) Alain in the newly proposed *Epicion* Small. Schumann recognized two sections in *Cynanchum*: *Cynoctonum* (E. Meyer) K. Schum. (= sect. *Cynanchum*), with completely to nearly completely fused corona segments, and *Vincetoxicum* (Moench) K. Schum., with basally fused to almost entirely free corona segments.

Woodson based six subgenera on characters of the inflorescence, corolla, and corona. However, the subgenera are difficult to interpret because of the existence of specimens assignable to the genus that are not accommodated by the key (see below), and because only a few representative species were listed for each. The inflorescences were said to be umbelliform in subg. *Metastelma* (R. Br.) Woodson (corolla lobes ascending or spreading) and subg. "Cleistolobus"³⁰ (corolla lobes inflexed and hoodlike) but racemiform to corymbiform in the other four. The corollas were reported to be urceolate in one of these, subg. *Tylodontia* (Griseb.) Woodson, and campanulate to rotate-subcampanulate in the other three. The segments of the corona were said to be broad, mostly connate, and emarginate in subg. *Metalepis* (Griseb.) Woodson, but elongate and free or only basally united in the other two. They were indicated as being acuminate and entire or with some very obscure lateral lobes in subg. *Mellichampia* (Gray) Woodson, but deeply bifid (i.e., with two long, linear lobes apically) in subg. *Ampelamus* (Raf.) Woodson.

As defined by Sundell (p. 11), subg. *Mellichampia* comprised 11 New World species and included as three (of four) sections "elements from three of Woodson's (1941) subgenera," subg. *Ampelamus*, subg. *Mellichampia*, and subg. *Metalepis*.³¹ Sundell described the subgenus as having an inner corona of five segments united basally into a short tube. However, it is difficult to evaluate the group because of the inclusion of plants that do not fit this description and the exclusion of others that do (see below).

Five species of *Cynanchum*, some of which appear not to be accommodated by any of the relevant treatments outlined above, occur in the southeastern United States. *Cynanchum laeve* (*Gonolobus laevis* Michx., *Enslenia albida* Nutt., *Ampelamus albidus* (Nutt.) Britton) is readily (and, among our species,

³⁰The name of this subgenus was not validly published by Woodson, since it was accompanied in 1941 neither by a Latin description or diagnosis nor by a reference to a previously and effectively published Latin description or diagnosis (i.e., it was not published in accordance with Art. 36.1 [ICBN, 1988], the effective date of which is January 1935). Therefore, it is enclosed in quotation marks here.

³¹Sundell was evidently the first to unite these three subgenera of Woodson (the names of which were published simultaneously), so the name he chose has priority.

uniquely) placed in Woodson's subg. *Ampelamus* by virtue of its racemiform inflorescences and deeply bifid corona segments. It was included in Sundell's subg. *Mellichampia* despite its entirely free corona segments, although because of this fact it was isolated in the monotypic sect. *Ampelamus* (Raf.) Sundell. (None of our other species was mentioned by Sundell.) *Cynanchum laeve* is unique among our representatives of the genus in having cordate leaves. (*Sarcostemma cynanchoides* Dcne., which enters our area in Arkansas and which is sometimes confused with *C. laeve*, has narrower cordate leaves.) It is found in alluvial thickets and old fields, as well as along stream banks and roadsides, from Pennsylvania to Kansas and generally southward to the Florida Panhandle and central Texas.

Cynanchum scoparium (*Amphistelma scoparia* (Nutt.) Small) has shallowly lobed coronas and would appear to belong to subg. *Metalepis* sensu Woodson. However, the lobes are not emarginate and the inflorescences are sometimes umbellate, so it is unclear to which subgenus in Woodson's system it belongs. On the basis of its basally connate corona segments, the species might also appear to belong to subg. *Mellichampia* sensu Sundell, and presumably to sect. *Metalepis* (Griseb.) Sundell. However, *C. scoparium* lacks the stipitate anther heads (they are sessile) that in part characterize this section, and the species was not treated by Sundell. In addition to its sometimes umbellate inflorescences and basally connate corona segments, *C. scoparium* is unique among our species of *Cynanchum* in several ways: the leaves (which are linear-lanceolate to linear but nevertheless petiolate) are deciduous relatively early, so the plants are often leafless or nearly so; the calyx lobes are obtuse (vs. acute); and the lobes of the corona do not exceed the anther head. *Cynanchum scoparium* is known from hammocks and pinelands in Beaufort County, South Carolina, and in central and southern Florida.

Cynanchum Northropiae (*Metastelma Northropiae* Schlechter; *Epicion Northropiae* (Schlechter) Small) is the only one of our species that can be placed in subg. *Mellichampia* sensu Woodson—an assignment primarily due to its racemose inflorescences. Its corona structure, however, suggests that it is more closely related to species in Texas and Mexico that, on the basis of umbellate inflorescences and ascending or spreading corolla lobes, are assignable in Woodson's system to subg. *Metastelma* (see Henrickson). In addition, the species has ovate to elliptic leaves with mucronate or acuminate (rarely emarginate) apices; corollas united in the basal third, with lobes that are densely pubescent adaxially; and clearly stipitate coronas, with segments that are distinct (and free from the corolla), narrowly lanceolate, radially (i.e., laterally) compressed, and adaxially grooved. The species is known from hammocks, pinelands, and cut-over lands in southern Florida, including the Keys, and in the West Indies.

Two of our species are assignable to subg. *Metastelma*, although on the basis of corona structure they appear to be related neither to *Cynanchum Northropiae* nor to the species in Texas and Mexico discussed above. *Cynanchum Blodgettii* (*Metastelma Blodgettii* Gray) has linear-lanceolate to linear leaves with acute and/or sometimes mucronate apices; corollas united in the basal third (or less) and urceolate (a condition partially characterizing subg. *Tylodontia*), with lobes densely pubescent adaxially (sometimes only near the apex); and sessile coronas

with lanceolate segments distinct from one another but basally adnate to the corolla and tangentially (i.e., dorsiventrally) compressed. The plants grow in hammocks and in rocky or sandy soil in pine and pine-palm woods in southern Florida, including the Keys. Although the species was reported from southern Texas by Small (1933), it was not treated by Correll & Johnston, and I have seen no specimens from the state.

Cynanchum angustifolium (*C. palustre* (Pursh) Heller; *Lyonia palustris* (Pursh) Small) is also assignable to subg. *Metastelma*. The leaves are linear with acute apices, but they are sessile and usually reflexed as well, two conditions not evident in our other species. In addition, *C. angustifolium* has glabrous, rotate-campanulate corollas divided nearly to the base, and stipitate to substipitate coronas with ovate to elliptic, distinct segments that are obtuse, retuse, or emarginate. The plants occur in coastal marshes with saline or brackish water and in sandy (probably moist) or marly soil of adjacent hammocks and dunes from North Carolina to southern Florida, including the Keys, and from there to Texas.

Several species of *Cynanchum*, including *C. laeve* (Bailey *et al.*), are cultivated in North America.

Standley & Williams's comment that *Cynanchum* in North America would be a good subject for dissertation research appears still to be true.

REFERENCES:

Under references for the Apocynineae, see BAILEY *et al.*; BROWN; CORRELL & JOHNSTON; SCHUMANN; SMALL, 1933; and STANDLEY & WILLIAMS.

Under references for the Asclepiadaceae, see SPELLMAN, 1975b; and WOODSON.

HENRICKSON, J. Notes on *Cynanchum* (Asclepiadaceae). *Sida* **12**: 91–99. 1987. [Three species in Texas and northern Mexico evidently do not enter the Southeast but appear to be related to *C. Northropiae*; very helpful illustrations.]

SUNDELL, E. The New World species of *Cynanchum* L. subgenus *Mellichampia* (A. Gray ex Wats.) Woods. (Asclepiadaceae). *Evol. Monogr.* **5**: 1–63. 1981.

5. *Sarcostemma* R. Brown, Mem. Wernerian Soc. **1**: 50. 1811.

Terrestrial (often in xeric habitats) to aquatic (sometimes rooted in standing fresh, brackish, or salt water), scandent and/or twining, perennial herbs (usually woody toward base) or suberect to prostrate subshrubs [or erect succulents] with white latex; axes and leaves glabrous or with various degrees of nonglandular pubescence [or sometimes glaucous]. Leaves opposite, sometimes caducous and the plants leafless or nearly so; blades ovate, elliptic, lanceolate, linear, or filiform [or scalelike], apices acute, acuminate, or mucronate, margins often revolute, bases attenuate, truncate, obtuse, or cordate [or hastate]; petioles distinct, without lateral appendages, bases and/or adjacent areas of stems usually with colleters. Inflorescences pedunculate [or sessile], few- to many-flowered, cymose but appearing umbellate [or racemose or corymbose], rarely with

both flowers and pedicel scars present, bracteate; pedicels longer than calyces, ebracteolate. Calyx about $\frac{1}{3}$ as long as corolla or less, free nearly to base, usually with nonglandular pubescence abaxially, glabrous adaxially; lobes acute, bases variously imbricate, with (or, reportedly, sometimes without) minute squamellae. Corolla much shorter than leaves, free nearly to base to united throughout the basal $\frac{1}{3}$, subrotate or subcampanulate [or sometimes campanulate or salverform], glabrous or with nonglandular pubescence abaxially, mostly glabrous adaxially; lobes valvate or variously imbricate, spreading [to nearly erect] basally, ascending, spreading, or reflexed apically. Outer corona [rarely absent] discoid, membranaceous or fleshy, mostly entire, basally adnate to corolla tube but apically free, forming an erect or ascending annulus. Inner corona exceeding to sometimes exceeded by anther head, substipitate or sessile, composed of distinct, mostly erect segments, each basally free from or (at least in *S. clausum*) adnate to annulus; segments 5, fleshy, vesicular, ovoid [or nearly spheroid]. Anther head cylindrical, immediately subtended by base of inner corona; anther wing slots directed outward. Anthers each with an apical, hyaline flap inflexed over style-stigma head, unappendaged abaxially. Style-stigma head short-cylindric, with flat, bilobed, or umbonate apex. Corpuscula partially exerted from anther head; translator arms arching downward; pollinia pendulous, completely fertile. Fruits follicular, 1 or sometimes [in some species, usually] 2 from each flower (the pair, when present, from single flower usually divergent less than 90° [to about 180°]), lance-ovoid, narrowly fusiform to fusiform-ovoid [or obclavate], acute to attenuate apically, dehiscent along adaxial suture, erect on erect pedicels to pendulous on pendulous ones; surface shallowly striate longitudinally, with various degrees of nonglandular pubescence. Seeds many, ovate-lenticular, each with a tuft of trichomes at apex; seed-coat surface rugose and/or papillate, lateral wings (at least in *S. clausum*) coarsely serrate. (Including *Ceramanthus* (Kunze) Malme, 1905; *Funastrum* Fourn., 1882; *Oxystelma* R. Br., 1809; *Philibertella* Vail, 1897; and *Philibertia* HBK., 1819.) LECTOTYPE SPECIES: *S. viminale* (L.) R. Br. (*Euphorbia viminalis* L.); see Holm, Ann. Missouri Bot. Gard. 37: 506. 1950. (Name from Greek, *sarkos*, flesh, and *stemmatos*, crown or wreath, probably in reference to the fleshy (and inflated) segments of the corona.)—MILK WITHE.

Considered here in the broadest sense, *Sarcostemma* is a genus of approximately 34 species, 22 in the New World (Holm) and about 12 in an area from Africa to Australia (Huber). There has been a great deal of confusion regarding *Sarcostemma* and several other genera with which it is here combined. Much of this has had to do with imprecise and/or inadequate treatment of the plants involved, shortcomings that are best appreciated by a brief consideration of their taxonomic history.

According to Holm, the most recent monographer of the genus, *Sarcostemma* originally included only succulent-stemmed, scale-leaved lianas of Asia and Africa with rotate corollas and both outer and inner coronas, the outer annular and the inner with five separate, inflated segments. In fact, however, in the protologue of *Sarcostemma*, Brown said nothing about succulence; indicated

that the stems were without leaves (although he was probably referring to plants with scale-leaves) or that the leaves were far apart (“foliis . . . distantibus”); reported the genus from eastern India, Africa, and Australia, as well as New Caledonia; and did not address the issue of inflation of the inner corona segments (he and many authors have referred merely to the fleshiness of the segments). Evidently, the summary provided by Holm was based on consideration of the species mentioned by Brown as they are now understood and/or on information that has come to light subsequently; generally, the same approach seems to have been taken in the remainder of his account. In addition to *Sarcostemma*, Brown also established *Oxystelma* R. Br. for plants of eastern India and possibly Australia with laminate foliage, rotate corollas, and single (i.e., only inner) coronas, without addressing the subject of corona-segment inflation.

From populations in the New World, Kunth (in Humboldt *et al.*) included in *Sarcostemma* some with lanceolate—albeit membranaceous—leaves and rotate corollas, and he erected *Philibertia* HBK. for others with cordate leaves and partly described with the phrase “corolla urceolato- (campanulato-?) rotata,” without addressing corona-segment inflation for either. Decaisne later described the corollas of *Sarcostemma solanoides* (HBK.) Dcne. (*Philibertia solanoides* HBK.), the only species included in *Philibertia* by Kunth, with the word “pelviformi” (i.e., basin or saucer shaped), which would seem to lie somewhere between rotate and campanulate.

Decaisne adopted a broad view of *Sarcostemma*, in which he recognized two sections. Section *Eusarcostemma* (= sect. *Sarcostemma*) included plants with rotate corollas and was divided into three unnamed groups, one comprising Old World species with scale-leaves (“aphylla” presumably in the sense that the foliage is not laminate), another of New World plants with linear to linear-lanceolate leaves (including *S. clausum* (Jacq.) Schultes, one of our two species), and a third of New World species with cordate leaves and deeply divided (but nevertheless rotate) corollas (including *S. cynanchoides* Dcne., the other of our two species). Section PHILIBERTIA (HBK.) Dcne. included New World species with cordate leaves and urceolate-rotate (possibly campanulate in the sense of others) corollas.

Despite employing a broad concept of *Sarcostemma*, Decaisne continued to recognize *Oxystelma* R. Br., in which he included Old World species with rotate corollas, as distinct. His description of *Oxystelma* differed significantly from Brown’s account of the genus in at least two respects. Decaisne referred to an annulus on the corolla tube (“fauce annulo . . .”), that is, an outer, annular corona as now interpreted, and described the segments of the (inner) corona, possibly for the first time, as being at least partially inflated. Even so, Decaisne did not mention this character state for *Sarcostemma*, even though he included in the latter our two species, each of which has inner corona segments that are clearly inflated.

Bentham (in Bentham & Hooker) included in *Sarcostemma* plants from Africa, Asia, and Australia with succulent stems, scalelike leaves (again, stems were said to be leafless), subrotate corollas, and at least sometimes subsaccate

(i.e., somewhat inflated) inner-corona segments. For reasons that are not entirely clear, he referred all of the New World species in question to *Philibertia*, which he described as having very widely campanulate to subrotate corollas and, at least occasionally, saccate segments of the inner corona. Significantly, he also noted an affinity between *Sarcostemma* and *Oxystelma*, and between *Oxystelma* and *Philibertia*; in fact, his descriptions of the last two genera were very similar. However, although no such terms were applied to *Oxystelma*, he indicated that the inner corona segments were at least sometimes saccate in *Philibertia*. (He also noted other differences in the segments.)

Fournier adopted very narrow generic concepts in establishing the New World genus *Funastrum* Fourn., which was described in part as having fleshy, vesicular corona segments; neither corolla shape nor the presence or absence of an outer corona was specified. Of the two species included, one actually belongs in *Cynanchum* L. according to Holm, while the other, *F. angustissimum* (Andersson) Fourn. (*Asclepias angustissima* Andersson, = *Sarcostemma angustissimum* (Andersson) R. Holm), of the Galapagos Islands, was indicated as having axillary umbels. Nevertheless, Holm (p. 535) reported that it is the only species of *Sarcostemma* with a "truly terminal inflorescence" (i.e., one that is not overtopped by sympodial growth; he actually considered the inflorescence to be terminal throughout the family), and on this basis he assigned it to the monotypic ser. *ANGUSTISSIMA* R. Holm.

Schumann also employed rather narrow generic concepts, maintaining in *Sarcostemma* only Old World species with prostrate or twining, succulent stems, scale-leaves (his "blattlose Sträucher"), and rotate corollas. He divided the genus into a sect. *Eusarcostemma* (= sect. *Sarcostemma*), with both outer and inner coronas (the former annular and, surprisingly, five- to ten-lobed; the latter sometimes partially vesicular), and a monotypic sect. *Sarcocyphula* (Harvey) K. Schum., with only an outer one.

Oxystelma and *Philibertia* were two other genera recognized by Schumann. The former included species in both Eastern and Western hemispheres, while the latter was used only for plants in the New World. Although the descriptions of the two genera were essentially identical (e.g., each was described as having twining, presumably nonsucculent stems; laminate foliage; rotate or campanulate corollas; and both outer and inner coronas, the former annular and the latter with vesicular segments), the key indicated that corollas were campanulate in *Oxystelma* and rotate in *Philibertia*. Schumann accepted *Funastrum* in exactly the same sense as Fournier had proposed it; that is, as including the same two South American species. According to Schumann, these are twining subshrubs with (presumably) nonsucculent stems, linear basal and scalelike upper leaves, rotate corollas, no outer coronas, and inner coronas with vesicular segments. It is surprising and often regarded as one of many unsatisfactory aspects of Schumann's classification that, within the Asclepiadeae, *Sarcostemma* and *Funastrum* were placed in two separate subtribes, while *Oxystelma* and *Philibertia* were included in a third.

Vail proposed *Philibertella* for the same American plants that had constituted *Philibertia* in Schumann's system, evidently because she felt the plants did not

adequately match Kunth's (in Humboldt *et al.*) description of *Philibertia* and because the only species Kunth had included in the genus was generally placed by that time in *Oxystelma*. Nevertheless, she indicated that corollas in *Philibertella* were either campanulate or rotate, so the distinction she attempted to make remains unclear.

Kunze established subg. CERAMANTHUS Kunze for New World members of *Sarcostemma* with urceolate corollas. Malme used the same name in elevating the group to generic status, even though it is at that rank a later homonym for a genus of Euphorbiaceae (i.e., *Ceramanthus* Hassk.) and several other generic names were available for the taxon that he envisioned (i.e., he included *Funastrum*, *Philibertella*, *Philibertia*, and others as synonyms).

Schlechter concluded that the New World species in question should be separated at the generic level and therefore resurrected *Funastrum* and *Philibertia*. Among other differences, *Funastrum* was indicated to have (compared to *Philibertia*) more rotate (vs. more campanulate) corollas, stipitate (vs. sessile or substipitate) anther heads (i.e., anther heads held above vs. immediately or nearly immediately subtended by inner coronas), and entire (vs. two-cleft) style-stigma head apices.

Following Decaisne in taking a broad view of *Sarcostemma*, Woodson united within it *Funastrum*, *Philibertia*, and others; *Oxystelma* was ignored because he was treating only New World plants. Although Holm formally treated only New World taxa in his revision, he adopted an even broader generic concept in adding *Oxystelma* to the taxa that had been included in *Sarcostemma* by both Decaisne and Woodson. Unlike Woodson, who did not subdivide the genus, Holm recognized three subgenera, one with three sections and another with five series. In view of the discussion above, his treatment seems most tenable and therefore is followed here.

Subgenus *Eusarcostemma* (Dcne.) R. Holm (= subg. SARCOSTEMMA), although based on sect. *Eusarcostemma* Dcne. (26 species, in both Eastern and Western hemispheres), was restricted to those species from Africa to Australia with succulent stems and scalelike leaves (i.e., the genus as originally delimited). Although the species included in this subgenus were not listed by Holm, the key indicated that the group was also characterized by rotate-subcampanulate corollas; an annular outer corona adnate to the filaments; and ovoid, vesicular (i.e., inflated) inner-corona segments.

The two other subgenera recognized by Holm included plants with nonsucculent stems and laminate foliage. Subgenus OXYSTELMA (R. Br.) R. Holm was characterized by campanulate corollas; an annular outer corona either adnate to the corolla or more or less obsolete; and variously ovoid or spheroid, vesicular inner-corona segments. It included sect. EUOXYSTELMA R. Holm (*Oxystelma* sensu Brown), with a single species in Africa and Asia, as well as sect. PENTACYPHUS (Schlechter) R. Holm (*Pentacyphus* sensu Schlechter) and sect. PHILIBERTIA (HBK.) Dcne. (*Philibertia* sensu Kunth), with two and six species, respectively, in South America.

Subgenus CERAMANTHUS Kunze (*Ceramanthus* (Kunze) Malme), comprising 14 New World species, corresponded to *Philibertia* as conceived by Bentham (i.e., the plants were said to have rotate-subcampanulate or salverform [rotate, as interpreted earlier] corollas), *Funastrum* of Fournier, and *Philibertella* of

Vail. It was otherwise indicated to have an annular outer corona (absent in one species) free from the corolla, and variously ovoid or spheroid, vesicular inner-corona segments. My observations of *Sarcostemma clausum* (Jacq.) Schultes and *S. cynanchoides* (discussed more fully below) indicate that in each the outer corona is adnate to the summit of the corolla tube. Near the apex it is sufficiently free from the corolla to form an annulus, which is fused with the bases of the inner-corona segments in *S. clausum* but free from them in *S. cynanchoides*. Subgenus CERAMANTHUS was divided into five series. One of these, ser. FLAVA R. Holm, included only a single, South American species with flowers lacking an outer corona. The other four differed primarily in characters of the inflorescence.

Two series of subg. CERAMANTHUS are represented in the southeastern United States, each by a single species. Series CLAUSA R. Holm (peduncles usually as thick as or thicker than subtending internodes, or lacking; when lacking, and sometimes otherwise, leaf bases obtuse to cuneate) included *Sarcostemma clausum* (leaves often caducous, elliptic to ovate). An extremely variable species (Holm listed nearly 60 synonyms, in six genera), *S. clausum* is found mostly in savannas or sandy areas in Mexico and northwestern South America but sometimes on wooded slopes, on floodplains, or rooted in standing water in Florida, the Greater Antilles, Central America, and eastern South America (Holm). The only other species in the series, *S. glaucum* HBK. of Panama, Colombia, and Venezuela, has salverform corollas with constricted tubes (vs. rotate-subcampanulate corollas with unconstricted tubes), and the plants are glaucous (vs. at least somewhat pubescent) throughout.

Series CYNANCHOIDES R. Holm (peduncles not as thick as subtending internodes, or lacking; when lacking, and sometimes otherwise, leaf bases cordate) included *Sarcostemma cynanchoides*, represented in our area, and eight other species distributed from the southwestern United States to central Argentina. Although in material I have seen from the Southeast the peduncle is often thinner than the subtending internode in *S. clausum* (in contrast to the usual condition in ser. CLAUSA), it is relatively even narrower in *S. cynanchoides*. Among specimens I have examined, the outer corona annulus is fused to the bases of the inner-corona segments in *S. clausum*, while these structures are free in *S. cynanchoides*.

Two subspecies were recognized in *Sarcostemma cynanchoides* by Holm. Subspecies *cynanchoides* was said to differ from subsp. *Hartwegii* (Vail) R. Holm in its broadly (vs. narrowly) lanceolate leaves with cordate or rarely truncate (vs. hastate or rarely truncate or obtuse) bases. Subspecies *cynanchoides* was indicated by Holm to grow in sandy soils of rivers and ditches and in rocky canyons from southern Arizona to the central parts of Oklahoma and Texas, as well as in adjacent parts of Mexico, and it has since been observed to enter our area in Arkansas. Smith indicated it for Franklin, Izard, and perhaps Pope counties, and I have seen a specimen (*Thomas & Reid 20640*, GH) from cliffs near the White River in Izard County that is assignable to this subspecies but misidentified as *Cynanchum laeve*. Subspecies *Hartwegii* occurs in more xeric habitats (e.g., dry, sandy, or rocky soils of arroyos and plains) and is distributed farther south and west, to central Mexico and southern California.

Sarcostemma cynanchoides subsp. *cynanchoides* begins to flower nearly two

months later than subsp. *Hartwegii* (Holm). Nevertheless, putative hybrids have been found in the area of geographic overlap between the two, mostly along the border between the United States and Mexico, from Arizona to western Texas. The low number of such hybrids might be related to the fact that the species is poorly collected in that area.

As defined here, *Sarcostemma* is most closely related to *Cynanchum* and *Blepharodon* Dcne. The latter includes about nine species and, according to Woodson, is perhaps divisible into a North American group of twining plants and a South American assemblage of erect, herbaceous ones. *Blepharodon* was considered to be in part intermediate in corona structure between *Cynanchum* and *Sarcostemma* by Holm (p. 504), who stated, without mentioning the groups proposed by Woodson, that the genus is divisible into one group with corona segments consisting of "two radially arranged, laminate lobes partially fused by their margins" and another in which such segments are "semi-vesicular." The flowers of *Blepharodon* and *Cynanchum* lack the outer (annular) corona characterizing *Sarcostemma*, although according to Holm they sometimes have structures that might be mistaken for one.

Despite the foregoing, the annular outer corona and the five inflated segments of the inner corona of the African and Asian genus *Pergularia* L. were considered by Holm to represent only superficial resemblances to *Sarcostemma*. Among other differences, *Pergularia* supposedly has a five-lobed, denticulate (vs. entire; however, see Schumann) outer corona and spurred (vs. not spurred) inner-corona segments.

The strong, flexible stems of *Sarcostemma clausum* (subg. CERAMANTHUS) are used in Guatemala for stringing fish and as a substitute for twine (Standley & Williams). Holm remarked that species of sect. PHILIBERTIA *sensu* Holm were often grown in English greenhouses during the nineteenth century and that those belonging to subg. SARCOSTEMMA *sensu* Holm are still commonly cultivated; in the latter group is *S. viminale*, which is sometimes sold as "*Euphorbia pendula*" (Bailey *et al.*).

REFERENCES:

Under references for the Apocynineae, see BAILEY *et al.*; BENTHAM & HOOKER; BROWN; DECAISNE; HUBER; HUMBOLDT *et al.*; SCHUMANN; SMITH; and STANDLEY & WILLIAMS.

Under references for the Asclepiadaceae, see FOURNIER and WOODSON.

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6. **Asclepias** Linnaeus, Sp. Pl. 1: 214. 1753; Gen. Pl. ed. 5. 102. 1754.

Terrestrial to semiaquatic (sometimes in brackish water), erect, perennial (or the introduced *A. curassavica*³² [and perhaps 2 other species] annual) herbs [or small shrubs] with white latex (only *A. longifolia* and *A. tuberosa* without latex); axes and leaves glabrous or with various degrees of nonglandular pubescence. Leaves usually decussate, less often irregularly alternate and/or subwhorled (whorled, usually in 4's, at node subtending inflorescence in *A. quadrifolia*); blades ovate, elliptic, lanceolate, linear, or filiform, apices acute, sometimes rounded, infrequently emarginate, sometimes mucronate, margins often revolute, bases attenuate, truncate, hastate, cordate, or auriculate; petioles sometimes very short and/or indistinct (especially when leaves linear or filiform), without lateral appendages, bases and/or adjacent areas of stems sometimes with a few small colleters. Inflorescences pedunculate, few- to many- [rarely single-]flowered, cymose but usually appearing umbellate, bracteate or rarely ebracteate; pedicels longer than calyces, ebracteolate. Calyx about 1/2 as long as corolla but usually much less, free nearly to base, glabrous or with various degrees of nonglandular pubescence abaxially, glabrous adaxially; lobes usually acute, bases sometimes slightly imbricate, usually with minute squamellae. Corolla much shorter than leaves, free nearly to base, essentially rotate (but see below), mostly glabrous abaxially and adaxially; lobes variously imbricate or sometimes valvate, reflexed or spreading proximally but reflexed or sometimes spreading or ascending (erect only in *A. pedicellata*) distally (when reflexed or spreading distally, often ascending apically). Outer corona absent. Inner corona exceeding to exceeded by anther head, stipitate to substipitate or sometimes sessile, composed of distinct, essentially erect or ascending (then sometimes basally deflexed) hoods (i.e., segments), each basally free from (but sometimes in contact with) corolla; lobules (i.e., small, erect, bifid or less often entire appendages) alternating with hood bases; hoods 5, fleshy, conduplicate (and therefore vessel- or tubelike), each open apically (openings not appressed against anther head) and exceeding to usually exceeded by horns (i.e., exserted, elongate, terete or laterally flattened, adaxially adnate appendages originating within hoods), or sometimes (in subg. ASCLEPIAS, subg. ASCLEPIODELLA) exceeding crests (i.e., nonexserted, ridgelike, rounded, adaxially adnate appendages originating within hoods), or less often (in subg. POLYOTUS) apparently unappendaged within, or (in *A. pedicellata*) each apically opened (openings not

³²This and epithets for many other species in the genus customarily have been given the feminine form, even though *Asclepias* would appear to be masculine and, in fact, was indicated as such by Stearn (Bot. Latin, 306. 1966). Nevertheless, as indicated by nearly all of the epithets appearing in *Species Plantarum* (1753), Linnaeus treated it as feminine. According to Art. 76.1 (ICBN, 1988), "a generic name retains the gender assigned by its author, unless this is contrary to botanical tradition," which, according to Note 1, "usually maintains the classical gender of a Greek or Latin word, when this was well established." The first example under this recommendation included names (other than *Asclepias*) "for which botanical usage has reestablished the classical gender despite another choice by Linnaeus." Therefore, it appears that if *Asclepias* is masculine according to "botanical tradition," Linnaeus should probably be overruled and the name should be treated as masculine.

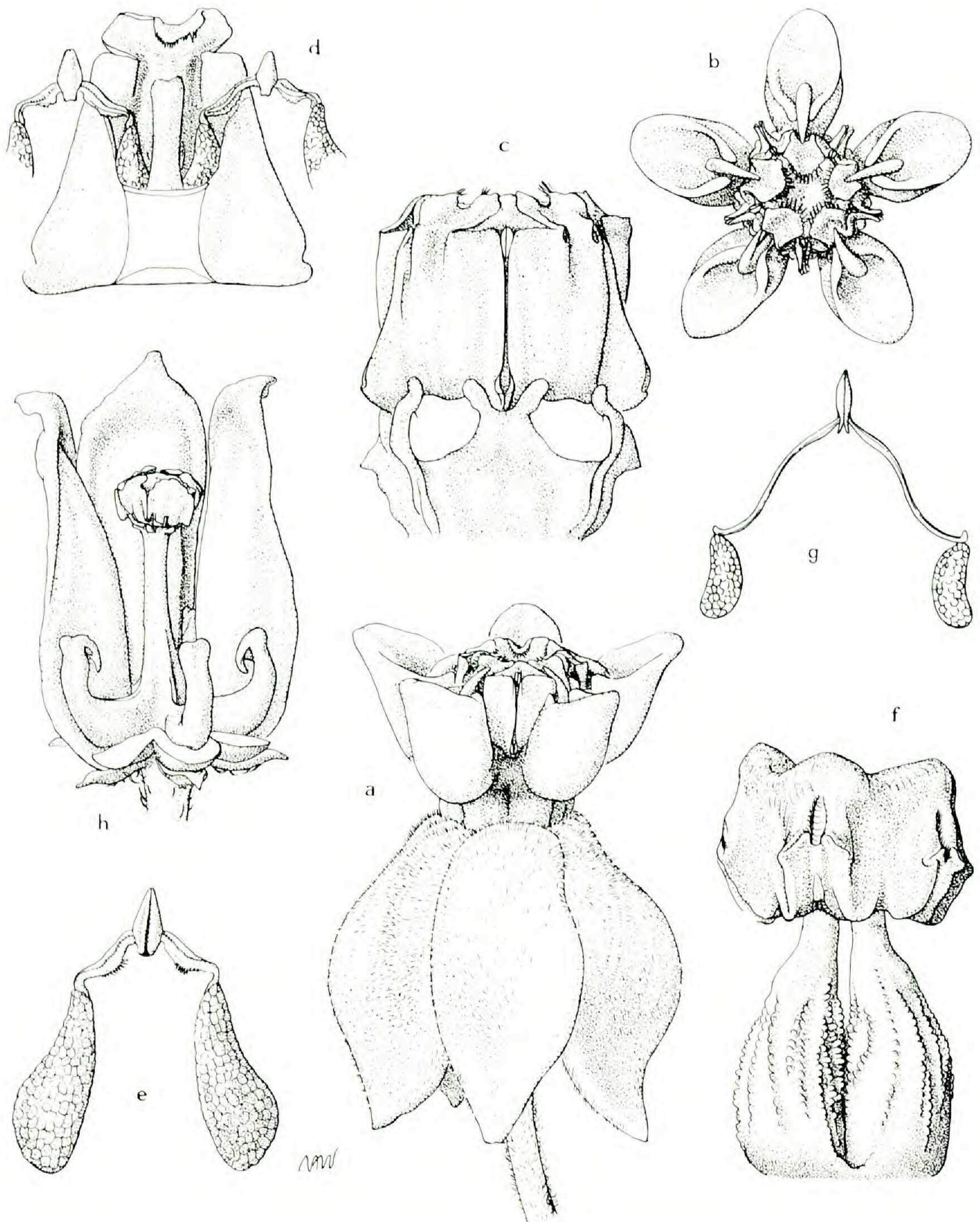


FIGURE 8. **Asclepias**. a–f, *A. syriaca*: a, flower (corolla lobes reflexed; corona stipitate [but saccate hoods partly concealing column]; hoods open at apex [openings not appressed against anther head] and here slightly exceeding exerted horns and anther head, abaxial surfaces exceeding those adjacent to anther head and not recurved apically, margins auriculate; anther head [excluding wings and terminal flaps] shorter than broad, immediately subtended by hoods; corpusculum at summit of outwardly projecting slot between wings of adjacent anthers), $\times 5$; b, flower, from above (hoods, with horns, opposite terminal, hyaline anther flaps over style-stigma head, alternating with corpuscula and outwardly projecting slots of adjacent anthers), $\times 5$; c, androecium (and, within, gynoecium) distal to level of adnation to corolla, with hoods removed (1 bifid lobule of corona flanked by 2 others; 1 outwardly projecting slot flanked by 2 others; 1 corpusculum; 1 hyaline flap terminating each of 2 anthers), $\times 12$; d, anther, adaxial side, with 2 pollinia (partly concealed) each connected by a translator arm, a corpusculum (surface not grooved), $\times 12$; e, anther, abaxial side, with 2 pollinia (partly concealed) each connected by a translator arm, a corpusculum (surface not grooved), $\times 12$; f, anther, lateral side, with 2 pollinia (partly concealed) each connected by a translator arm, a corpusculum (surface not grooved), $\times 12$; g, anther, abaxial side, with 2 pollinia (partly concealed) each connected by a translator arm, a corpusculum (surface not grooved), $\times 12$; h, anther, adaxial side, with 2 pollinia (partly concealed) each connected by a translator arm, a corpusculum (surface not grooved), $\times 12$.

appressed against anther head) but inwardly geniculate (and the openings therefore concealed) and apparently unappendaged within, or (in subg. *ACERATES*) each apically opened (openings appressed against anther head) and exceeding crests or apparently unappendaged within, or (in subg. *ANANTHERIX*, subg. *ASCLEPIODORA*) each apically enclosed (by conduplication) and apparently unappendaged within. Anther head cylindrical, immediately subtended by or (in *A. pedicellata*) held well above and separated by a long stipe from base of inner corona; anther wing slots directed outward. Anthers each with an apical, hyaline flap inflexed over style-stigma head, unappendaged abaxially. Style-stigma head cylindrical, with flat or depressed apex. Corpuscula partially exerted from anther head; translator arms arching downward; pollinia pendulous, completely fertile. Fruits follicular, 1 or very rarely 2 from each flower (the pair, when present, from single flower usually divergent less than 90°), narrowly fusiform to infrequently fusiform-ovoid or broadly ovoid, acute to attenuate-caudate apically, dehiscent along adaxial suture, erect on deflexed pedicels (the latter therefore S-shaped) or less frequently erect on erect ones (pendulous on pendulous pedicels in *A. perennis*); surface smooth or with elongate tubercles [or spines], nearly glabrous to rarely with dense nonglandular pubescence. Seeds many, ovate-lenticular, each with (or without, in *A. perennis*) a tuft of trichomes at apex; seed-coat surface usually smooth, lateral wings usually entire and more or less flat, sometimes crenate and/or undulate. (Including *Acerates* Ell., 1817; *Anantherix* Nutt., 1818; *Asclepiodella* Small, 1933; *Asclepiodora* Gray, 1877; *Biventraria* Small, 1933; *Oxypterix* Greene, 1897; *Podostemma* Greene, 1897; and *Podostigma* Ell., 1817. Excluding *Gomphocarpus* R. Br., [preprinted 1810] 1811; *Schizoglossum* E. Meyer, 1838; and *Xysmalobium* R. Br., [preprinted 1810] 1811.) LECTOTYPE SPECIES: *A. syriaca* L.; see Hitchcock & Greene, Prop. Brit. Bot. 136. 1929. (According to Linnaeus [Critica Botanica, p. 76, 1737; p. 60 in A. Hort, English translation, 1938], named for the physician Aesculapius; *Asclepias* listed by Linnaeus [Critica Botanica, p. 102, 1737; p. 83 in A. Hort, English translation, 1938] as an ancient Greek name, but later [Philosophia Botanica, p. 141, 1751] as a name provided by Tournefort; according to Morse, 1985b, named for Asclepios, the Greek god of healing.)—MILKWEED.

Considered here in neither the broadest nor the narrowest of senses, *Asclepias* includes more than 100 North and Central American as well as “less than a dozen poorly differentiated” southeastern South American species (Woodson, 1954, p. 28).

and another translator arm to 1 pollinium (partly drawn) from adjacent anther, $\times 12$; e, pollinarium, abaxial side (1 pollinium from each of 2 adjacent anthers, 2 translator arms, and 1 corpusculum with surface grooved for attachment to insects; pollinia and translator arms oriented as in intact anther, $\times 16$; f, gynoecium, with androecium removed (the 2 carpels mostly free in ovule-bearing and stylar regions, united apically into style-stigma head; 1 vertical furrow, of 5, of style-stigma head [center], with stigmatic surface [below] and position of corpusculum at summit of gynoecial walls of stigmatic chamber), $\times 12$. g, *A. connivens*: pollinarium (cf. “e”), with characteristically long translator arms, $\times 12$. h, *A. pedicellata*: side view of flower with 2 corolla lobes removed (sepals spreading; corolla lobes erect; corona sessile, hoods ascending, open but geniculate apically; anther head held well above hoods), $\times 5$.

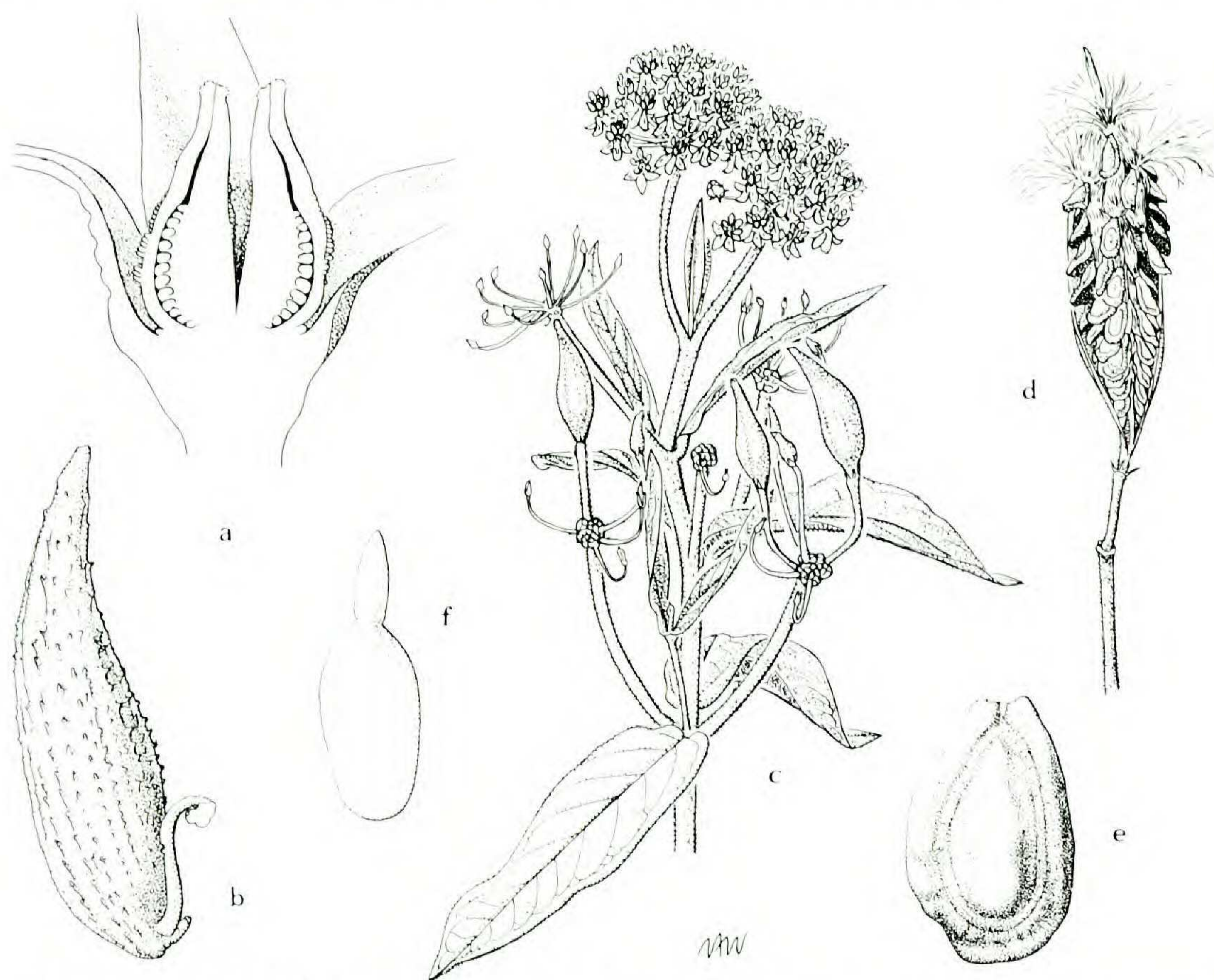


FIGURE 9. *Asclepias*. a, b, *A. syriaca*: a, flower with very young fruit, cut longitudinally, after fall of corolla, androecium, and style-stigma head but before disappearance of calyx and probable abortion of 1 follicle, showing 3 calyx lobes, 2 with squamellae at base, 2 very young follicles, mostly free, with axile placentation and numerous developing seeds, $\times 8$; b, nearly mature follicle, erect on deflexed pedicel, with aborted carpel at lower right, $\times \frac{1}{2}$. c-f, *A. incarnata* subsp. *pulchra*: c, distal part of stem with some inflorescences and infructescences paired at nodes, young follicles erect on erect pedicels, $\times \frac{1}{2}$; d, mature, dehiscent follicle, releasing seeds with apical tufts of trichomes, $\times \frac{1}{2}$; e, seed, apical tuft of trichomes removed, seed coat winged laterally, $\times 3$; f, embryo, somewhat expanded from soaking in water (oriented as in "e"), $\times 4$.

Here excluded from *Asclepias* is *Gomphocarpus* R. Br., which was tentatively included by Woodson (1954). According to Pobedimova, the latter includes about 100 species in central and northern Africa, about ten in Central and South America, and one in Arabia. Although in both genera the segments of the inner corona are conduplicate (hood shaped), those in *Gomphocarpus* lack the adaxial appendages (horns or crests) characteristic of but not universally present in *Asclepias* (some of our species at least appear to lack them; see below). *Asclepias* may also be related closely to two genera of tropical and southern Africa with laminate (i.e., flat, not conduplicate) inner-corona segments. These structures have and do not have adaxial appendages in *Schizoglossum* E. Meyer (about 25 species) and *Xysmalobium* R. Br. (about ten species), respectively (see Schumann). Good informally recognized four assemblages of Asclepiadaceae with representatives in both the Old and New worlds; one of them was composed entirely of these four genera.

Here included in *Asclepias* are a number of segregate genera that were recognized, for example by Small, as being monotypic and confined to the Southeast (*Anantherix* Nutt., *Asclepiodella* Small, *Oxypterix* Greene, and *Podostigma* Ell.), monotypic and geographically centered in but not limited to the Southeast (*Biventraria* Small), or composed of several species and relatively widespread in North and Central America (*Acerates* Ell. and *Asclepiodora* Gray).

According to Woodson (1954), the natural distributions of 27 species of *Asclepias* include at least part of the southeastern United States, while those of five others (*A. asperula* (Dcne.) Woodson, *A. Engelmanniana* Woodson, *A. linearis* Scheele, *A. oenotherioides* Cham. & Schlecht., and *A. Sullivantii* Engelm.) were shown to approach this area closely from the west; *A. Sullivantii* has since been recorded from Arkansas (Smith). The showy-flowered *A. curassavica* L., native to Central America and/or the Antilles and/or South America, has been widely introduced in the tropics and subtropics of both the Old and New worlds, including, in North America, parts of the Coastal Plain, from Florida to Texas, and southern California.³³ In most cases, these 33 species can be readily distinguished using relatively few vegetative and floral characters (see below).

Woodson (1954) recognized nine subgenera (one of which included nine series), 108 species, and 14 subspecies in his treatment of North and Central American plants. Of these, seven or possibly eight subgenera and seven series are represented in the southeastern United States. Although Woodson (1954) considered these species groups to be mostly unnatural, they are nevertheless used here for purposes of presentation and species identification. They are presented in a different order for logistical purposes, and in some cases the characteristics defining them have been modified to reflect my studies of the 33 species that occur or possibly occur without cultivation in the Southeast. Lynch & Martin have suggested that cardenolide profiles obtained from thin-layer chromatography would be of value to the infrageneric classification of *Asclepias*.

Nearly all of the herbarium specimens I have seen are readily identified using criteria presented below. A much longer discussion, and in some cases liquid-preserved or fresh material as well, would be needed to identify the remainder. Vegetative and floral characters have been used instead of ones involving the fruits, at least in part because the latter are not nearly as variable within the genus, are unknown for some species, and are not present on most specimens. Because the following is limited to features discernible on herbarium specimens,

³³Whether or not *Asclepias curassavica* is truly naturalized anywhere in North America is not entirely clear. Long & Lakela stated that it is a pantropical weed that has become naturalized on the Coastal Plain from Florida to Texas and in California, and Wunderlin included it among plants "native or naturalized" in central Florida. However, it was listed neither among native and naturalized species of the Florida Panhandle (Clewell) or Georgia (Jones & Coile), nor among "some exotic ornamental species that persist after the abandonment of land" (Clewell, p. 1) included with the former. MacRoberts listed the species among those growing without cultivation in Louisiana but did not indicate whether or not the plants were reproducing. Correll & Johnston (p. 1233) referred to it in their treatment of plants in Texas simply as an "almost ubiquitous waif" of the tropics and subtropics in the New World, and Munz (p. 457) indicated that in California it is occasionally cultivated and escaped, "as at Mandeville Canyon, Santa Monica Mts."

several characters often used in identification (e.g., color of flowers; shape of abaxial surfaces of hoods) have been avoided.

Asclepias pedicellata Walter (*Podostigma pedicellata* (Walter) Vail), of the Coastal Plain from Florida to North Carolina, is our only representative of subg. *PODOSTIGMA* (Ell.) Woodson. The species appears to be unique within the genus in its erect or nearly erect corolla lobes (vs. reflexed or less often spreading and/or ascending). Furthermore, whereas the anther head is held above and separated from the hoods by a long section of the column in *A. pedicellata* (see FIGURE 8h), it is immediately subtended by them in all other species in the genus, including the other three included in subg. *PODOSTIGMA* by Woodson (1954). In fact, although Woodson (1954, p. 48) stated that the anther head is "borne on a stipe . . . high above the hoods" in subg. *PODOSTIGMA*, it is only slightly elevated in these other three species, which in this respect grade into subg. *ASCLEPIODORA* (Gray) Woodson.

The hoods are closed at the apex in species of two of our subgenera. In the monotypic subg. *ANANTHERIX* (Nutt.) Woodson they are spreading or erect at the base and converge above the anther head, and the coronas are stipitate to substipitate (i.e., the column is visible between the bases of the hoods and the corolla). The single representative of subg. *ANANTHERIX*, *Asclepias connivens* Baldwin (*Anantherix connivens* (Baldwin) Feay), occurs on the Coastal Plain in the northern half of Florida and in the southern parts of Georgia, Alabama, and Mississippi. (For the pollinarium of *A. connivens*, see FIGURE 8g.)

In subg. *ASCLEPIODORA* (Gray) Woodson (seven species, two in the Southeast) the hoods are deflexed at the base but otherwise ascending, although not convergent above the anther head, and the coronas are sessile (i.e., the column is not visible between the bases of the hoods and the corolla). *Asclepias viridis* Walter (*Asclepiodora viridis* (Walter) Gray), with hoods that are about one-half or less as long as the spreading or ascending corolla lobes, is known from all of the Southeastern States except the Carolinas, although it appears to be most common from Nebraska and Missouri south to eastern Texas and Louisiana and is sporadic east of the Mississippi River. The distribution of *A. asperula*, with hoods that are nearly as long as the spreading or ascending corolla lobes, is centered even farther west, in the southwestern United States, and very closely approaches but evidently does not include Arkansas.

The hoods are open at the apex (see FIGURE 8a, b) in species of the other five subgenera under discussion, although the openings are appressed against the anther head and/or column in subg. *ACERATES* (Ell.) Woodson (five species, three in the Southeast). The coronas are sessile in *Asclepias viridiflora* Raf. but clearly stipitate in *A. hirtella* Woodson and *A. longifolia* Michx. (*Acerates longifolia* (Michx.) Ell., *Acerates floridana* (Lam.) Hitchc., *Acerates delticola* Small).

Asclepias viridiflora is widespread in the eastern two-thirds of the United States as well as in some adjacent parts of Canada, and it occurs throughout the Southeast; however, its distribution appears to be centered in the lower Midwest and adjacent parts of the Central Plains, and it has only recently been reported from Florida (Anderson). *Asclepias hirtella* (inflorescences lateral, hemispheric to nearly spherical; hoods with small crest at base within) is geographically centered in the lower Midwest but is known from all of our states

except Florida and the Carolinas, whereas *A. longifolia* (inflorescences mostly terminal, less than hemispheric; hoods unappendaged within) is distributed along the Coastal Plain from Louisiana to Maryland.

The hoods are open at the apex and the opening is not appressed against the anther head in the remainder of the 33 species of the Southeast. The hoods at least appear to lack internal appendages in subg. *POLYOTUS* (Nutt.) Woodson (three species, one or possibly two in the Southeast). The hoods are apically trilobed in *Asclepias stenophylla* Gray, with the shorter middle lobe evidently representing an otherwise completely adnate horn, whereas they are apically unlobed and truly unappendaged in *A. Engelmanniana*. *Asclepias stenophylla* is geographically centered in eastern Nebraska, western Missouri, and Oklahoma east of the panhandle and is probably fairly common in northwestern Arkansas. *Asclepias Engelmanniana* is distributed more to the west, from which it approaches but apparently does not enter the Southeast.

Each hood has an internal appendage in the remainder of the 33 Southeastern species. In most the appendage is an exserted horn (exceeded by to exceeding the hoods), while in some it is a nonexserted crest that probably represents a reduced horn. The coronas are sessile or very nearly so in two of the subgenera involved, subg. *ASCLEPIODELLA* (Small) Woodson and subg. *PODOSTEMMA* (Green) Woodson. The hoods do not exceed the anther head in subg. *ASCLEPIODELLA*, a group of seven species, two of which are represented in the Southeast by plants with linear to filiform leaves. The hoods of *Asclepias cinerea* Walter (southern South Carolina to northwestern and central Florida) have horns, while those of *A. Feayi* Chapman (*Asclepiodella Feayi* (Chapman) Small) (restricted to peninsular Florida) have crests.

The hoods exceed the anther head by between about one- and two-thirds their lengths in the six species of subg. *PODOSTEMMA*, one of which, *Asclepias oenotherioides* Cham. & Schlecht., with broader than linear leaves, is distributed from eastern Texas (near to but evidently not in Louisiana) to northwestern Mexico, southward to Costa Rica.

The coronas are not always completely sessile in *Asclepias cinerea* (subg. *ASCLEPIODELLA*) and *A. oenotherioides* (subg. *PODOSTEMMA*). The plants involved therefore might be confused with members of the last subgenus to be considered, subg. *ASCLEPIAS*, except that the hoods in *A. cinerea* have very prominent, erect, marginal auricles that clearly exceed the rest of the hood and those of *A. oenotherioides* are much narrowed toward the base.

The coronas are stipitate or sometimes substipitate in subg. *ASCLEPIAS*, although in some cases the column is hidden by deeply saccate and/or deflexed hoods. Woodson (1954) recognized nine series³⁴ in the subgenus, seven of which are represented in the southeastern United States. In three of these (sers. "Incarnatae," "Tuberosae," and "Exaltatae") the anther heads, excluding wings and terminal flaps of the anthers, are usually about as long as to longer than

³⁴The names of these series were not validly published by Woodson (1954), since they were accompanied neither by a Latin description or diagnosis nor by a reference to a previously and effectively published Latin description or diagnosis (i.e., they were not published in accordance with Art. 36.1 [ICBN, 1988], the effective date of which is January 1935). Therefore, they are enclosed in quotation marks here.

broad, while in four (sers. "Roseae," "Syriacae," "Macrotides," and "Purpurascens") they are usually shorter than broad.

Subgenus ASCLEPIAS ser. "Incarnatae" includes about 16 species, four or perhaps five of which occur in the Southeast. The hood margins are without auricles and the leaves are opposite in all of these except *Asclepias verticillata* L. (throughout our area and the eastern United States in general, also in adjacent parts of Canada, and sporadically to as far west as Arizona), in which the hood margins are usually auriculate and the leaves on individual plants are whorled (in 3's, 4's, or sometimes 5's) or, infrequently, usually whorled and otherwise opposite. The hoods clearly exceed the anther head in *A. curassavica* (see above) but range from slightly exceeding to clearly being exceeded by it in three other species. The inflorescences are usually paired at the upper nodes and solitary below in *A. incarnata* L., while in *A. perennis* Walter (leaves broader than linear) and *A. linearis* Scheele (leaves linear to filiform) they are nearly always solitary. *Asclepias incarnata* is widespread in the eastern three-fourths of the United States and adjacent parts of Canada but is most concentrated in the area north of ours. It seems to be fairly common in Florida, eastern Tennessee, and the Carolinas but is poorly known if not absent in other parts of the Southeast. *Asclepias perennis* has a curious and possibly artifactual distribution, involving the Coastal Plain from Texas to South Carolina and the lower Ohio River valley. *Asclepias linearis* is endemic to southeastern Texas, according to Woodson (1954) and Correll & Johnston. Although Small indicated that it extends into our area to as far east as Alabama, the species was listed for neither Louisiana (MacRoberts) nor Arkansas (Smith).

In subg. ASCLEPIAS sers. "Tuberosae" and "Exaltatae" the hood margins have auricles and the leaves are opposite or irregularly alternate. The auricles are closer to the hood bases and the hoods clearly exceed the anther head in ser. "Tuberosae." This series is represented in our area by three species, one, *A. tuberosa* L. (with irregularly alternate leaves), widely distributed (to as far west as Arizona) but primarily eastern North American (including southern parts of Canada), and two (with opposite leaves) of the Coastal Plain (from eastern Texas to southern New York). *Asclepias rubra* L. (absent in peninsular Florida) has acute hood apices and broadly ovate to lanceolate leaves, while *A. lanceolata* Walter (common throughout Florida) has rounded hood apices and linear-lanceolate leaves.

The auricles are closer to the hood apex (but usually do not exceed the rest of the hood by as much as they do in *Asclepias cinerea* of subg. ASCLEPIODELLA), and the hoods never exceed the anther head by much (they range from slightly exceeding it to being slightly exceeded by it) in ser. "Exaltatae." Two of the nine species in this group are represented in the southeastern United States. *Asclepias exaltata* L. (leaf-blade bases not clasping stem, peduncles usually lateral and much shorter than subtending leaves), of the northeastern United States and adjacent Canada, enters our range along the Appalachian Mountains to about as far south as northern parts of Georgia and perhaps Alabama. *Asclepias amplexicaulis* Small (leaf-blade bases clasping stem, peduncles usually terminal and much longer than the subtending leaves) is widespread in the

eastern two-thirds of the United States (and probably occurs in southern Canada), including our area, although it is not known to occur in peninsular Florida.

The basis for Woodson's (1954) inclusion of two of our species and 11 others in ser. "Roseae" is not altogether clear. Among our representatives of this series, the abaxial surface of each hood is exceeded by the surfaces adjacent to the anther head and is not recurved apically in *Asclepias tomentosa* Ell. (hoods slightly to clearly exceeded by anther head) but clearly exceeds the surfaces adjacent to the anther head and is recurved apically in *A. obovata* Ell. (hoods clearly exceeding anther head). Both species are known from scattered localities along the Coastal Plain from eastern Texas to the Carolinas, except that *A. obovata* (*Acerates obovata* (Ell.) Eaton) has been reported from neither North Carolina nor peninsular Florida; Clewell (p. 251) indicated that it is a ruderal in the Florida Panhandle in "Jackson and Gadsden to Bay Cos."

The abaxial surface of each hood exceeds the surfaces adjacent to the anther head but is not recurved apically in sers. "Syriacae," "Macrotides," and "Purpurascentes." The marginal auricles of the hood generally are sharply incised and acute at the apex in ser. "Syriacae" but shallow and broad in sers. "Macrotides" and "Purpurascentes."

Four of the 11 species belonging to ser. "Syriacae" occur in the southeastern United States. *Asclepias viridula* Chapman has linear to filiform, opposite leaves and appears to be endemic to northern Florida and perhaps adjacent parts of Georgia, while our other three species have wider, nearly always opposite leaves and are more widespread. *Asclepias humistrata* Walter (leaf-blade bases clasping stem, leaves opposite) occurs on the Coastal Plain from Louisiana to North Carolina, while *A. quadrifolia* Jacq. (leaf-blade bases not clasping stem, leaves whorled or subwhorled at or near first node beneath inflorescence but otherwise opposite) and *A. syriaca* L. (leaf-blade bases not clasping stem, leaves opposite) mostly grow in the northeastern quarter of the United States and adjacent parts of Canada, including in our area northern Arkansas and the Appalachian Mountains to about as far south as Georgia and Alabama. *Asclepias syriaca* is widespread in the northeastern quarter of the United States and adjacent parts of Canada; it may be native to the northern parts of our range but naturalized farther south (see Woodson, 1954; Broyles & Wyatt).

One of the eight species included in ser. "Macrotides," *Asclepias Michauxii* Dcne. (*A. angustifolia* Ell.), occurs in the Southeast. It is endemic to the Coastal Plain from Louisiana to South Carolina, including peninsular Florida, and can be distinguished from our species of ser. "Purpurascentes" by its irregularly alternate, filiform to linear (vs. opposite, broader than linear) leaves.

Three or four of a total of eight species comprising ser. "Purpurascentes" occur in the Southeast. The hoods are acute to narrowly rounded apically and exceed the anther head by more than half their length in *Asclepias purpurascens* L. and *A. Curtissii* Gray (*Oxypterix Curtissii* (Gray) Small). *Asclepias purpurascens* (plants erect) occurs primarily in the northeastern quarter of the United States and in adjacent parts of Canada but enters our range in parts of Louisiana, Arkansas, Tennessee, and North Carolina, whereas *A. Curtissii* (plants decumbent) is endemic to peninsular Florida. The hoods are broadly rounded to

truncate apically and exceed the anther head by less than half their length in *A. variegata* L. (*Biventraria variegata* (L.) Small) and *A. Sullivantii*. *Asclepias variegata* (leaf-blade bases not clasping stem) is widespread in the area southeast of a curve from about southern New England to Arkansas and eastern Texas but has not been reported from peninsular Florida. *Asclepias Sullivantii* (leaf-blade bases clasping stem) is mainly distributed in the southern half of the Midwest (reported also from southern Canada) and enters our area only in Jackson County, Arkansas (Smith).

Woodson (1954) recognized infraspecific taxa in only three of the 33 species mentioned above. On the basis of morphological, ecological, and geographic evidence, two subspecies, both of which occur in the Southeast, were recognized in *Asclepias incarnata*. Subspecies *pulchra* (Ehrh.) Woodson (plants conspicuously pubescent instead of essentially glabrous, leaves broader than in the typical element, and other minor differences) occurs along the Atlantic Coast (as well as in adjacent, inland areas) in Florida and from Maine and Nova Scotia to North Carolina, where it frequently grows in brackish tidal marshes, while subsp. *incarnata* has a more inland distribution (essentially throughout the Midwest, but with widely scattered stations elsewhere) and is only associated with fresh water. The possibility that the morphological characteristics of subsp. *pulchra* are induced by saline environments apparently has not been investigated.

Woodson (1954) recognized four subspecies in *Asclepias tuberosa* based on leaf shape and to some extent geography; three of them are known from the Southeast. However, he had earlier demonstrated "extremely active" introgression among them (Woodson, 1953), and I have observed them to be morphologically indistinct. Two subspecies were treated in *A. asperula*, the more eastern of which, subsp. *capricornu* (Woodson) Woodson (sessile to subsessile instead of clearly pedunculate inflorescences, in addition to other differences) was reported from a locality in McCurtain County, Oklahoma, within about 40 miles of Arkansas and was said sometimes to spread to pastures from more natural habitats.

According to Woodson (1954), few North American species of *Asclepias* occur at elevations above 2000 meters, and a minority (perhaps as many as 12 of ours) are distributed as far north as Canada. Most of the species discussed above appear to be optimally adapted to relatively open, dry habitats such as pine barrens, flatwoods, prairies, glades, thickets, and sand dunes. In addition to *A. incarnata* (see above), other species at least sometimes occurring in moister habitats than these include *A. asperula* (desert swales), *A. connivens* (marshes, low areas in woods), *A. curassavica* (moist places), *A. Engelmanniana* (washes, bottoms, swales), *A. exaltata* (moist woods and meadows), *A. longifolia* (swamps, low pine lands), *A. perennis* (low swampy ground), *A. rubra* (bogs, marshes, wet meadows, low pine barrens), and *A. syriaca* (alluvial bottoms); *A. lanceolata* is found in wet pine barrens and low glades, as well as in both fresh water and brackish marshes. Although Woodson (1954) stated that, among the 33 species in our area, only *A. curassavica*, *A. syriaca*, and possibly *A. incarnata* are to any extent weedy, he indicated that *A. amplexicaulis*, *A. Feayi*, *A. hirtella*, *A.*

obovata, *A. oenotherioides*, *A. purpurascens*, *A. Sullivantii*, and *A. viridiflora* often spread to roadsides, old fields, and/or railways from more natural habitats.

Natural hybrids between species of *Asclepias* appear to be very rare, presumably because of mechanical isolation effected by sets of rather exact pollination requirements. Natural and fertile artificial hybrids have been reported in subg. ASCLEPIAS between *A. exaltata*, of ser. "Exaltatae," and *A. syriaca*, of ser. "Syriacae" (see Kephart & Heiser; Kephart *et al.*). Included by Woodson (1954) in a list of nine apparent but untested hybrids are some specimens combining the characteristics of *A. amplexicaulis* (ser. "Exaltatae") and *A. humistrata* (ser. "Syriacae"), from Florida; *A. amplexicaulis* and *A. syriaca*, from New York; and *A. syriaca* and *A. viridiflora* (subg. ACERATES), from Indiana. Other specimens intermediate between one of the 33 species in the Southeast and another species were also reported. These involve *A. verticillata* and the extraregional *A. pumila* (Gray) Vail (both of ser. "Incarnatae"); *A. syriaca* and the extraregional *A. speciosa* Torrey (ser. "Purpurascentes"), between which hybrids were obtained experimentally (see also Thomson & Wagner); and *A. oenotherioides* and the extraregional *A. Emoryi* (Greene) Vail (both of subg. PODOSTEMMA), between which intermediates are frequent in nature. Plants grown by Moore (1946b) from seeds probably resulting from natural pollinations and produced by plants of *A. speciosa* growing in experimental plots with *A. syriaca* were intermediate in flower, stem, and leaf character states at least in part defining these two species.

Moore (1946b) attempted to produce artificial hybrids involving several of the species discussed here, for the most part unsuccessfully. Although ovary enlargement, presumably resulting from successful fertilization, was observed for crosses of *Asclepias tuberosa* (ser. "Tuberosae") with *A. Sullivantii* (ser. "Purpurascentes"), *A. curassavica* (ser. "Incarnatae") with *A. syriaca* (ser. "Syriacae"), and *A. curassavica* with *A. speciosa* (ser. "Purpurascentes"), the fruits and seeds did not mature. Moore's list of even-less-successful artificial crosses (i.e., those after which no ovary enlargement was observed) included various other combinations involving these species and *A. incarnata*, *A. Sullivantii*, and *A. tuberosa*, to which Woodson (1954) added *A. curassavica* crossed with *A. quadrifolia* (ser. "Syriacae") and *A. purpurascens* (ser. "Purpurascentes"), *A. verticillata* crossed with *A. incarnata* (both of ser. "Incarnatae"), and others involving these and two extraregional species.

Cytological evidence has not been useful in the evaluation of putative hybrids, primarily because all of the species involved are of the $2n = 22$ cytotype. Otherwise it has been of interest in the sense that the chromosomes of *Asclepias curassavica* are significantly smaller than those of the other species investigated by Moore (1946b), all native to North America, consistent with the idea that this species is a more distantly related introduction to the continent.

Even though fruits are not especially variable within the genus, the spatial relationships between the follicle and pedicel appear to be of phylogenetic importance (Woodson, 1954). During fruit maturation in most species, the pedicel becomes deflexed while the follicle remains erect. Despite being common within the genus and (supposedly) in the rest of the Asclepiadeae (but see

generic descriptions here), this condition was thought to be relatively advanced because it is unknown in the rest of the Asclepiadaceae. The production of erect follicles on erect pedicels or pendulous follicles on pendulous ones is more characteristic of the family as a whole, and although less common in *Asclepias*, was therefore considered to be more primitive than erect follicles on deflexed pedicels. Erect or pendulous pedicels are most frequent in subg. ASCLEPIAS, while erect follicles on deflexed pedicels are unknown in ser. "Incarnatae" (cf. FIGURE 9c); these taxa were considered on the basis of floral morphology to be the most primitive within their genus and their subgenus, respectively.

Despite the foregoing, erect follicles on erect pedicels or pendulous follicles on pendulous ones occur as well in other subgenera of *Asclepias* and in other series of subg. ASCLEPIAS. Among the Southeastern species, erect follicles and pedicels are known in *A. incarnata*, *A. linearis*, *A. curassavica*, and *A. verticillata* of ser. "Incarnatae," as well as in *A. quadrifolia* and *A. viridula* of ser. "Syr-iacae," *A. Michauxii* of ser. "Macrotides," *A. cinerea* and *A. Feayi* of subg. ASCLEPIODELLA, and *A. stenophylla* of subg. POLYOTUS. Among this same group, pendulous follicles and pedicels (and, incidentally, noncomose seeds) occur only in *A. perennis* of ser. "Incarnatae"; the fruits of *A. Curtissii* and *A. pedicellata* are evidently unknown. Pendulous follicles and pedicels also occur in extraregional species of ser. "Roseae" and subg. PODOSTEMMA. Woodson (1954) considered most of these species to be primitive within their respective series and subgenera on the basis of floral morphology.

The precise location of nectar production in flowers of *Asclepias* has been controversial. The hoods were generally accepted as the site, probably because of the conspicuous accumulation of nectar there, until, according to Galil & Zeroni (1965), Stadler concluded in 1886 that it was produced in the stigmatic chambers as well. More recent workers reverted to the original idea, and some even regarded the horn as its ultimate source. Working with *A. curassavica* in Israel, Galil & Zeroni (1965) showed that nectar accumulates both in the hoods and in the stigmatic chambers, although histochemical and other tests demonstrated that it is produced only in the latter (see also Schnepf & Christ). Using very small pipettes and a solution of ten percent sucrose with a few drops of india ink, they also established that liquid passes from the base of each stigmatic chamber into the two nearest hoods through passageways largely defined by the lobules of the corona and the bases of the two adjacent anthers; that is, each lobule causes the nectar to flow from the base of the stigmatic chamber laterally into the bases of the two nearest hoods, instead of down the column between them.

The hoods evidently allow for accumulation of the massive amounts of nectar required by insect visitors large enough both to fly the great distances often separating individual plants and effectively to engage the pollination mechanism involved, which in various ways favors outcrossing. In many cases during nectar-feeding visits, one (or more) of an insect's appendages (usually a leg or a head part) becomes wedged in the abaxial groove of the corpusculum, to which it is sometimes guided from below by the outwardly projecting, apically narrowing slot (and associated, upwardly oriented bristles) between the anther wings. Visitors of sufficient strength depart for another flower intact, carrying

away the corpusculum with attached translator arms and pollinia, while others remain trapped or leave behind the wedged part because the pollinia are too heavy and/or too tightly held within the anthers.

According to most accounts, the translators begin to rotate within a few minutes after removal from the flower, continuing until the wide axes of the pollinia are perpendicular to their original orientation and their more sharply convex sides are adaxial. This action orients pollinia such that the same pollinator behavior that effected their removal from the anthers of one flower can result in their insertion, one at a time, into the outwardly projecting anther wing slots of another, with their more sharply convex sides inward, adjacent to the receptive surfaces within the stigmatic chambers. Because such effective insertion of pollinia into the slots is substantially more likely after translator rotation, delay of the latter until after the pollinator is likely to have departed for another individual is generally thought to promote outcrossing. However, my observations of *Asclepias syriaca* indicate that the translator arms are under tension while the pollinarium is in place, and that they begin to rotate immediately upon removal.

Pollinator activity at a flower visited after translator rotation in the pollinarium being transported sometimes results in the insertion of one pollinium of the pair into a stigmatic chamber, usually from somewhat below. As the insect moves its trapped appendage toward the apex of the flower in attempting to free itself, the inserted pollinium may become detached by pressure exerted against the anther wings forming the anther slot, so that the inserted pollinium remains in the stigmatic chamber. At other times the translator arm or the insect's appendage to which it is attached becomes wedged in the abaxial groove of the resident corpusculum, forcing detachment of the inserted pollinium, perhaps along with the translator arm and sometimes the insect's appendage as well. Continued pollinator movement may also result in removal of the resident pollinarium in the manner described above. If an inserted pollinium remains attached to its translator arm and to the insect's appendage and if either of the latter is wedged in the resident corpusculum upon its removal, the inserted pollinium will be removed along with the resident pollinarium. Successive repetitions of such occurrences often result in chains of pollinaria.

Wyatt (1976) advanced the idea that inserted pollinia are more likely to remain so when the associated resident pollinarium (especially the corpusculum) is still intact and in place. (For extraregional species, see also Lynch.) That removal of resident pollinaria is possible without upsetting a previous insertion was offered to explain unexpected observations that the numbers of insertions into chambers associated and not associated with intact resident pollinaria are frequently about equal. However, Wyatt (1978) later provided experimental evidence from manipulated flowers in natural populations of *Asclepias tuberosa* in North Carolina that insertions were in fact more numerous in chambers associated with intact resident pollinaria. He believed that these findings confirmed his original hypothesis that the corpusculum helps to ensure that the translator arm will be broken and the inserted pollinium will remain behind. Such a mechanism presumably favors outcrossing, and it perhaps simultaneously decreases the wasteful placement of pollinia, to the extent that

insertion of pollinia would be less likely into the stigmatic chambers of flowers that have already been pollinated (because one or more of the five corpuscula would have been removed).

Most evidence suggests that Hymenoptera generally are more frequent pollinators of *Asclepias* flowers than are Lepidoptera, and that the latter in turn are more frequent than Coleoptera, Diptera, and Hemiptera. Such was indicated in Robertson's (1928) compilation in Illinois, in which visitors with pollinaria, among others, were listed for each of eight species represented in the Southeast (*A. incarnata*, *A. purpurascens*, *A. Sullivantii*, *A. tuberosa*, *A. longifolia*, *A. syriaca*, *A. verticillata*, and *A. viridiflora*); ruby-throated hummingbirds (*Archilochus colubris*) were reported to visit the flowers of the first four of these, although none was observed with pollinaria.

More detailed and recent studies also have indicated that, in general, Hymenoptera are more important than Lepidoptera in the pollination of *Asclepias* flowers (for exceptions, see Bierzychudek; Wyatt, 1980a). Wyatt (1976) found that, in comparison with localities farther east, many pollinaria were removed but few inserted among 15 populations of *A. tuberosa* in eastern Kansas and western Missouri that were visited by relatively small numbers of Hymenoptera (mostly bumblebees, honeybees, and wasps) and large numbers of Lepidoptera (primarily monarch, swallowtail, and sulfur butterflies). Although butterflies (especially monarchs) were frequent visitors to flowers of *A. syriaca* in a coastal area in Maine, bumblebees were usually ten to 20 times more numerous and carried pollinaria four times as often (Morse, 1985b).

Morse (1985b) also noted that, although at night flowers of *Asclepias syriaca* were quite fragrant, produced considerably more nectar than during the day, and were visited by large numbers of moths, Lepidoptera were responsible for only five to 25 percent of the total number of pollinial insertions (day and night) (but see Willson & Bertin). Nevertheless, Bertin & Willson demonstrated with *A. syriaca* and *A. verticillata* that, although insect visitors and pollinial insertions were less frequent at night, seed-set and "pod-set" were equal or greater, suggesting that nocturnal pollinators may be superior to diurnal ones. Bertin & Willson also suggested that the predominance of diurnal visitors may be due largely to the introduction of the honeybee (*Apis mellifera*).

Data provided by Willson, Bertin, & Price indicated that for *Asclepias verticillata* Hymenoptera were more frequent carriers of pollinaria than were Lepidoptera at three of four study sites in Illinois, and that whereas the former were more important than the latter at the least disturbed site (70 percent vs. 0 percent of all vectors, respectively), the opposite was true at the most disturbed site (15 percent vs. 51 percent).

Pollinaria of three species of *Asclepias* represented in the Southeast were found by Kephart (1983) on a wide variety of insects collected from experimental plantings in Indiana. Although close associations between individual plant and pollinator species were not evident, *A. syriaca* was associated with a narrower range (Hymenoptera, including bees in *Apis* and *Bombus* and wasps in *Polistes* and *Sphex*; Lepidoptera in *Cisseps*, *Danaus*, and *Speyeria*; Coleoptera in *Chauliognathus*; and Diptera and Hemiptera in unspecified genera) than either *A. incarnata* (bees in *Apis*, *Bombus*, and *Xylocopa*; wasps in *Cerceris*,

Myzinum, *Polistes*, and *Sphex*; Lepidoptera in *Battus*, *Cisseps*, *Danaus*, and *Speyeria*; Coleoptera in *Chauliognathus*; and Diptera and Hemiptera in unspecified genera) or *A. verticillata* (all taxa mentioned above for *A. syriaca* and *A. incarnata* except *Speyeria*; also wasps in *Entypus*).

Beare & Perkins's field observations of two populations of *Asclepias tuberosa* in south-central Oklahoma revealed the existence of fruiting and nonfruiting individuals. The slots over the stigmatic chambers were significantly wider than the pollinia were thick in plants that developed fruits, while the reverse was true of those that did not (pollinial thickness was constant). Fruiting individuals clearly had greater numbers of pollinial insertions and greater percentages of intact pollinaria as well, supporting Wyatt's (1976) hypothesis that the likelihood of pollinial insertion is enhanced by the presence of intact pollinaria. Dimorphism in slot width would favor outcrossing to the extent that flowers with narrow slots are much less likely to be pollinated in general (3.45 percent vs. 96.55 percent insertion) and therefore to be self pollinated in particular. Evidently, nonfruiting plants act primarily as pollinial donors.

A variety of explanations, including infrequent, ineffective, or disruptive insect visitation, resource limitations for developing ovules and fruits, and/or various levels of physiological incompatibility, have been offered to account for the low percentage (ca. 1 percent according to Woodson, 1954) of flowers that develop into mature fruits in species of *Asclepias*.

That pollination does not limit fruit-set has been suggested by various studies of *Asclepias syriaca* in North America in which the percentage of flowers with inserted pollinia has ranged from about 65 among natural populations in southeastern lower Michigan (Sparrow & Pearson) to about 95 among experimental plants in southeastern Ontario (R. J. Moore, 1947). However, much lower (but unspecified) values were obtained for *A. tuberosa* in natural populations throughout much of the eastern half of the United States, perhaps at least in part because pollinia of this species are thought to be removed but not inserted by some species of butterflies (Wyatt, 1976).

Low insertion rates in *Asclepias tuberosa* might also be due to nectar-robbing ants, on which pollinaria of this species have been observed in large numbers (Wyatt, 1976). Indeed, insertions were more frequent among inflorescences of *A. curassavica* in Costa Rica from which ants were excluded (Wyatt, 1980a). Thus, nectar-robbing can reduce both the number of pollinaria and the amount of nectar available to legitimate pollinators, some of which, especially in *A. curassavica* (Galil & Zeroni, 1965), have been observed to remove nectar directly from the stigmatic chambers of flowers in which the hoods were emptied, resulting in the relatively ineffective placement of pollinaria on head parts (see also Fritz & Morse). Wyatt (1980a) suggested that the opposite, sessile, amplexicaulous leaves of several species (e.g., *A. amplexicaulis*, *A. humistrata*, *A. Sullivantii*) might reduce the number of ants reaching inflorescences and thereby enhance sexual reproduction.

Fruit-set among species of *Asclepias* may also be limited by physiological incompatibility systems and resource limitation. Sparrow & Pearson found that only flowers pollinated with pollinia from distant plants or from clones producing fruits of a different type (see Sparrow) developed mature fruits. All

other pollen was either completely ineffective or resulted in fruit abortion at various stages early in development. Willson & Price (1980) demonstrated that various aspects of seed and fruit production by uncultivated plants of *A. incarnata*, *A. syriaca*, and *A. verticillata* in Illinois were generally increased by the addition of nitrogen, phosphorus, and potassium and were decreased by defoliation and perhaps by shading.

Not only is fruit-set in *Asclepias* infrequent overall, but almost invariably only one of the two carpels per flower develops into a mature fruit. Sparrow & Pearson reported that in artificially pollinated flowers of *A. syriaca*, pollen tubes from a single stigmatic cavity enter only a single style, suggesting that in general the ovules of one carpel may be fertilized only by pollen in two adjacent chambers, and that those in the other might receive pollen tubes only from the other three. If this is indeed true, fertilization of both carpels would require pollinial insertion in both groups of stigmatic chambers.

The rarity of natural hybrids between species of *Asclepias*, despite the close geographic and/or ecological proximity of many, has usually been attributed to mechanical isolation effected by a specific fit between stigmatic chambers and pollinia (i.e., the "lock and key" of many authors, the "tongue-in-groove" of Beare & Perkins) of individual species (see especially Holm). Vector specificity has not been invoked because pollinaria of several diverse species have often been observed on individual insects.

Kephart & Heiser studied pollination in natural and experimental populations of three sympatric, mostly self-incompatible species of *Asclepias* in Indiana, *A. incarnata*, *A. syriaca*, and *A. verticillata*. Despite statistically significant differences among the species in the sizes of both stigmatic chambers and pollinia, effective pollinations were observed for all combinations except those involving the relatively large pollinia of *A. syriaca* and their insertion into the comparatively small stigmatic chambers of *A. incarnata* and *A. verticillata*; pollinaria of *A. tuberosa* (and other species) were also occasionally found in the stigmatic chambers of all three species. Thus, Kephart & Heiser concluded that, while such mechanical barriers to hybridization are neither as effective nor as significant as was previously thought, they and other pre-pollination barriers may nevertheless sometimes contribute to decreased interspecific pollination.

Indeed, Macior's field observations of *Asclepias incarnata*, *A. syriaca*, and *A. verticillata* in southeastern Wisconsin suggested that other floral characteristics affect the positioning of pollinaria on pollinators. Poor footing on flowers and wide spaces between hoods (as in *A. syriaca*) were positively correlated with pollinial placement on insect pulvilli, while good footing and narrow spaces (as in *A. incarnata* and *A. verticillata*) seem to favor placement on the tarsal claws subtending them, at least in part because the tarsus in such cases is less likely to be drawn through the stigmatic chambers directly from below. Macior also implied that behavioral diversity among insects might in some cases decrease the likelihood of cross-pollination. That the foregoing may be, nevertheless, ineffective in preventing the misplacement of pollinia is indicated by his observations of chains composed of pollinaria belonging to two or more of these and other species.

The failure of all of 279 attempted artificial crosses involving *Asclepias incarnata*, *A. syriaca*, and *A. verticillata* as reported by Kephart (1981) indicates that post-pollination barriers are considerably more important than those discussed above. Pollen-tube penetration into the styles and, in some crosses between *A. incarnata* and *A. verticillata*, into the ovules as well suggests late pre- or early post-fertilization, physiological incompatibility. The evidently weaker barrier between *A. incarnata* and *A. verticillata* may imply greater genetic similarity between them, consistent with their separation from *A. syriaca* at the level of series by Woodson (1954).

Many insects are rendered unpalatable by ingestion of plants in several species of *Asclepias* (as well as other Apocynineae), due primarily to the presence of cardiac glycosides in the latex (e.g., see Brower *et al.*; Duffey & Scudder; Erickson; Euw *et al.*; Isman *et al.*; Rothschild; Seiber *et al.*). The resemblance of the palatable viceroy butterfly to the unpalatable monarch is perhaps the best-known and most frequently taught example of Batesian mimicry.

Bailey and colleagues listed about 20 of our species of *Asclepias* as being cultivated in North America. Some are grown as ornamentals, while others have been evaluated as potential crop plants for a variety of purposes (see family discussion). Several species in the southeastern United States were used by "Indians" in various ways: latex for chewing gum; bark fiber to make rope and string; buds, young shoots, leaves, and fruits for food; and dried roots for medicine (Uphof). *Asclepias curassavica* is one of the most common weeds in the lowlands of Central America, where the latex is placed in the nostrils to treat head colds and in cavities to relieve toothache; it is also sometimes used internally as an emetic and purgative and is believed to be useful in the treatment of poisonous bites (Standley & Williams). The many uses of *A. incarnata*, *A. syriaca*, and *A. tuberosa* have been discussed by M. I. Moore.

In addition to the literature discussed above, see annotations of the references below for information about overall biology (Bhowmik & Bandeen), general ecology (Blakley & Dingle; Price & Willson, 1976, 1979; Wilbur, 1976), pollination biology and breeding systems (Boyden; Chaplin & Walker; Corry, 1883a, 1883b; Dailey *et al.*; Frost; Galil & Zeroni, 1969; Kephart, 1979; Morse, 1981, 1982; Morse & Fritz, 1983, 1985; Pleasants & Chapin; A. K. Southwick & Southwick; E. E. Southwick; Willson & Price, 1977), fruit and seed production (Bell; Bookman, 1983a, 1983b, 1984; R. J. Moore, 1946a; Morse, 1987; Queller, 1983, 1985; Wilbur, 1977), seed germination (Baskin & Baskin; Farmer *et al.*; Jeffery & Robison; Kis; Morse & Schmitt; Oegema & Fletcher), and the taxonomic significance of latex (Moyer).

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